WISCONSIN STRATIGRAPHY AT PORT TALBOT ON THE NORTH SHORE OF LAKE ERIE, ONTARIO

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GENERAL PLEISTOCENE GEOLOGY

Most of the area north of Lake Erie is covered by Pleistocene deposits in thickness of 100 to 300 feet, except for both ends of the lake where bedrock is shallower. The surface drift is generally considered to be of Cary and Mankato age (Glacial Map of North America, 1945).

In order to obtain a better idea on the Pleistocene stratigraphy of the area north of Lake Erie, the writer has examined hundreds of exposures along the central portion of the lake, between Romney and Port Rowan, Ontario. A brown clayey till, interbedded and covered by lacustrine deposits, was found to be the principal material. This till is in one layer in the eastern half of the area studied, but it consists of two or three towards the west. All three till beds have similar colour, texture and lithologic composition (Dreimanis and Reavely, 1953, p. 238–239). They appear to be deposited by the same ice lobe during the oscillatory retreat. A common name, the "upper till," have been applied to these till beds because each of them is exposed on the surface farther north of Lake Erie. A similar clayey till extends also south of the lake (White, 1951, p. 971).

A deeper sandy till has been found either in exposures (Dreimanis and Reavely, 1953, p. 239) or reported by well logs through the entire area studied, and it has been called the "lower till." Similar sandy tills underlie the surface drift in northern Ohio (Shepps, 1953, p. 43).

No organic deposits or soils have been found between the upper and the lower till in Southwestern Ontario. Therefore, these two tills are considered as deposits of the last, Wisconsin, glaciation.

THE PORT TALBOT AND PLUM POINT SECTIONS

While examining Lake Erie cliffs half a mile southwest of Port Tlabot (fig. 1) in October 1951, the author and his students found a previously unknown organic layer below the lower till. In figure 2, which represents this section, the "upper till" and associated lacustrine deposits are shown as units (h), (i), (j) and (k), but the "lower till" and the related stratified drift as (e), (f) and (g); the organic gyttja layer is in (c). A still older till (a), texturally similar to the lower till (g), and a related varved clay (b) were found underneath the gyttja.

A search for more organic remains revealed wood in the till (g) at Plum Point, one mile south west of the Port Talbot gyttja exposure.

The following beds are exposed there (beginning with the top layer):

lacustrine clay, equivalent to (k) or (i) + (k) in figure 2................25 feet
clayey "upper till," equivalent to (h)....................................18 feet
gravel...0–1
                                                foot

silty "lower till," equivalent to (g), with a SE–NW and ESE–WNW fabric;
    drag-folds overturned towards WNW; ratio of calcite to dolomite in till

matrix: 0.7; wood was found in the middle portion of this till........10–20 feet

fine sand, probably equivalent to (d), exposed above lake level only at the

S. W. side of the section.. 0–10. feet

These two exposures with organic remains have been compared with many others and, both combined, were considered as the most complete Wisconsin sections along the north shore of Lake Erie. Therefore they have been studied in great detail.
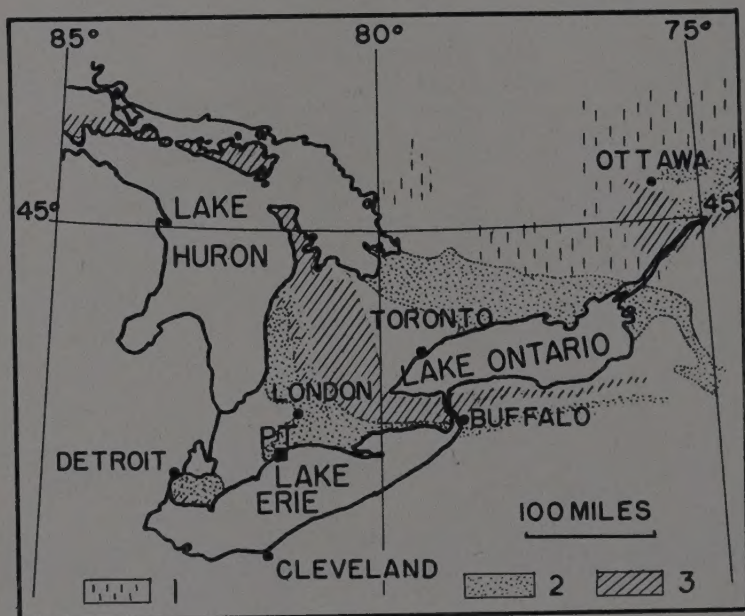

FIGURE 1. Map showing the location of Port Talbot, Ontario (P. T.) and the principal areas of carbonate bedrock:
1—scattered exposures of Precambrian crystalline limestone and dolomite,
2—Palaeozoic limestone,
3—Paleozoic dolomitic rocks.

Supplemental Information on the Port Talbot Geologic Section

A well, 103 feet above the lake level and 220 feet inland from the edge of the cliff, was drilled by A. Lather in 1955 (fig. 2 for its location). Its log (table 1) reveals at least three more till layers below the lake level.

The three foot thick layer of fine sand (depth 123 to 132 feet) may correspond to the sand (d) or silt (c) of the lake bluff on figure 2. The variance in depth of this sand (30 to 40 feet deeper than at the lake shore) may be due to folding by glacial thrust, as the layers (b) to (f) and the basal portion of the "lower" till (g) is folded, overthrusted or sheared at many places along the lake shore.
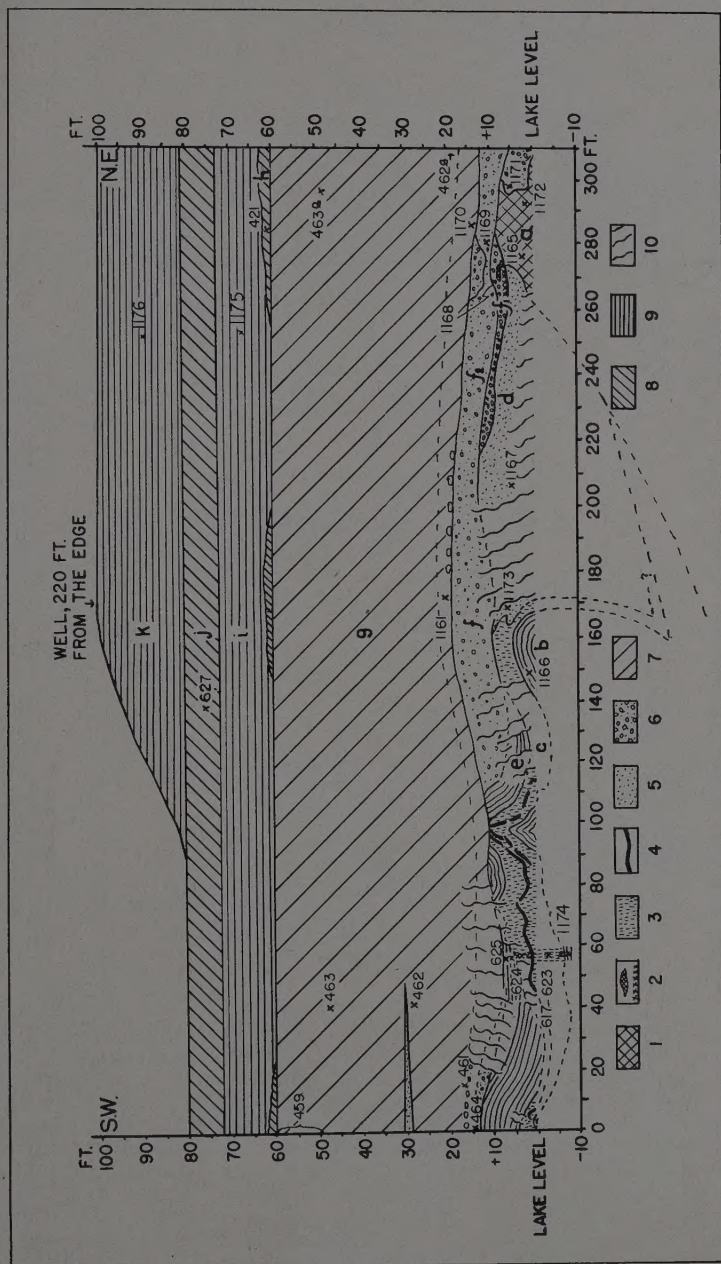
FIGURE 2.   Geologic section along the lake Erie bluff half a mile SW of Port Talbot, Ontario.
Legend: 1—till (a), 2—till (f), 3—silt (c), 4—gyttja (c_4 and c_6), 5—sand, 6—gravel, 7—till (g), 8—"upper till" (h) and (j), 9—lacustrine clay (b), (e), (i) and (k), 10—slump, x—locations of samples and their reference numbers.

An excavation at the 56 ft. point of figure 2 and augering down to 7 feet below the lake level revealed the following details of the bed (c):

d —lacustrine clay, stratified   2 feet
— — — — — — — — — — — — — — — unconformity
c_6—silt, faintly stratified, yellow, calcareous; with a few tiny shells of
    molluscs   3 feet
c_5—gyttja, dark brown to dark gray, with visible plant remains and
    some shells of molluscs; calcareous   0.2–0.3 feet
c_4—calcareous gyttja, light gray, similar to (c_5) and grading into it, but
    with more calcite and more molluscs   0.2–0.3 feet
c_3—silt, stratified, yellow; with some plant remains and molluscs,
    calcareous   1.3 feet
— — — — — — — — — — — — — — — unconformity
c_2—silt, stratified; gray, with dark lamina, relatively rich in fine organic
    matter; becomes yellow when exposed to air   4 feet
c_1—sandy silt, gray   3 feet
— — — — — — — — — — — — — — — unconformity
b   varved clay   at least one
                                                           foot

TABLE 1

Well Log, Port Talbot interstadial site

| Well log, as reported by A. Lather | | | | Probable |
Thickness ft.	Depth ft.	Material	Geological Interpretation	correlation with figure 2
45	0–45	Clay	Lacustrine clays and upper tills	(h), (i), (j), and (k)
84	45–129	Hardpan	Till	(g) and (f)
3	129–132	Fine sand, with water, that rose to 100 ft. below surface	Fine sand or silt	(d) and/or (c)
13	132–145	Hardpan	Till(?)	(a)
38	145–183	Gray clay	Lacustrine clay(?)	older
20	183–203	Hardpan	Till(?)	than
12	203–215	Pink clay	Lacustrine clay (?)	(a)
16	215–231	Hardpan	Till(?)	
3	231–234	Dundee "big lime"	Bedrock: middle Devonian limestone, Dundee formation	

TEXTURE, LITHOLOGY, ICE-FLOW DIRECTION

Grain-size distribution, lithologic composition and till fabric has been studied in the Port Talbot area by methods described in Dreimanis and Reavely (1953). In addition, calcite was differentiated from dolomite while determining the carbonate content of silt and clay (-200 mesh fraction). Results of examinations from the section shown on figure 2 are summarized in tables 2 and 3. Supplemental information about the "upper till," equivalent to the layers (h) and (j), and the "lower till," equivalent to (f_1) and (g), may be found in Dreimanis and Reavely (1953), and Dreimanis, Reavely, Cook, Knox and Moretti (1957).

Till (a).—This is the lowermost exposed till in the area studied. It has been found only at one place (fig. 2). This till is gray and resembles the "lower till" (g). It has also a similar mechanical composition with sand and gravel dominating over silt and clay and is highly calcareous (43 percent carbonates). The till (a)

TABLE 2

Lithology of pebble and sand fractions—Port Talbot interstadial site

Reference letter	File No.	Material	Pebbles 5–25 mm. — Ign. & Metam.	Sandstone & siltstone	Limestone	Chert	Dolomite	Shale	Coarse sand 0.5–1 mm. — Feldspar	Mafic min.	Quartz	Sandstone & siltstone	Limestone	Chert	Dolomite	Shale	Percentage of heavy minerals in sand: 0.15–0.8 mm.	Palaeozoic / Precambrian — Pebbles	Coarse sand	Limestone / Dolomite — Pebbles	Coarse sand	Purple garnet / Red garnet in sand 0.15–0.8 mm. †
j	627, 380	Second bed of "upper till"	5	3	24	3	3	63	6	2	7	4	7	2	5	67	1.4	19	5.7	8	1.4	0.9–3.0
h	379, 421	First bed of "upper till"	9	15	21	2	10	43	5	+	7	5	9	2	4	68	1.5	10	7	2.1	2.3	mode: 1.0
	459	+40 ft.	21	2	41	9	26	1	13	8	16	7	35	2	20	1	2.35	3.8	1.7	1.6	1.8	
	463	+33 ft.	23	0	54	2	20	1	15	39 9	22	5	31	61	17	1	2.75	3.4	1.6	2.7	1.8	
	462	+13 ft.	25	1	45	7	22	0									3.40	3.0	1.2	2.0		
g	461	+3 ft.	23	0	47	1	29	0	17	45 7	22	5	30	55 3	14	2		3.4	1.2	1.6	2.1	0.2–1.0
	464	+1 ft.	17	8	46	5	24	+										4.9	1.2	1.9		mode: 0.7
	1161	+1 ft.															3.55					
	1170	+1 ft.															2.75					
f₂	1169	gravel	18	6	42	4	22	0										4.8		1.9		
	1169a	gravel	27	5	39	2	27	1										2.7		1.5		
	1171	gravel	19	5	42	5	28	0										4.3		1.5		
f₁	1168	till	25	7	43	4	19	2	18	7	22	3	32	3	12	3	4.50	3.0	1.1	2.2	2.7	0.7
d	1167, 1173	pebbles in sand	19	1	29	3	46	+										4.3		0.6		
a	1165	lowermost till	22	2	34	6	36	0	19	9	29	1	21	3	17	1	3.47	3.5	0.8	0.9	1.2	0.6
	1172	till	21	3	32	9	34	1										3.8		0.9		

†Ratios quoted from Dreimanis, Reavely, Knox, Cook and Moretti (1957); they are based upon 28 heavy mineral determinations along the north shore of Lake Erie.

differs from all the later tills along the north shore of Lake Erie by a higher content of dolomite. Dolomite exceeds calcite five times in the −200 mesh fraction, but both of them are in a relatively equal amount in sand and among pebbles. Crushing of glacial drift during its transport increases the amount of rock flour with the distance from its source. Therefore, the relatively greater dominance of dolomite over calcite in the finer grain sizes of the till (a) than in its coarser components suggests a distant source, at least for some of the dolomite.

The regional trend of the ice flow which deposited this till may be concluded from the heavy mineral composition. Heavy minerals were examined by G. H. Reavely, who found their association essentially similar to that of the Erie "lower till" (g) (Dreimanis *et al.*, 1957, p. 160). The only noticeable difference was in the low percentage of garnets: 4 percent in (a) but more than 15 percent in (g). The heavy mineral content, if compared with the source areas on the Canadian shield (Dreimanis *et al.*, 1957, fig. 1), suggests that the glacier has traversed the Grenville province. Thus it must have come from the north east or north.

Extensive source areas of dolomite, required by the highly dolomitic till matrix, are along both the above ice-flow directions (fig. 1). The most distant source is the Ordovician Beekmantown dolomite of the St. Lawrence lowland. The dolomitic Silurian and Devonian rocks of Southwestern Ontario are relatively closer. As the till layer (a) has been deformed by ice pressure at the interstadial site, its fabric at this place is not reliable for deciphering the glacial movement, which existed during the deposition of the till. Additional regional lithologic and fabric studies are still necessary for final conclusions of the ice-flow direction and source areas of this till.

Layers (b), (c) and (d).—All these three layers are considered lacustrine deposits; (d) may be also fluvial. Their stratigraphic sequence is most completely exposed in the central portion of figure 2. The varved clay (b) may be seen also in other places along the water level of Lake Erie. Its varves are approximately one inch thick, and they have been faulted considerably, probably by glacial pressure.

The bed (c) consists of very calcareous silt (50 percent carbonates) with a lens of gyttja in the middle. The gyttja layer is doubled along the west limb of the fold at 90 to 100 feet mark (fig. 2). As both the gyttja and silt are sheared at this place, the doubling may be considered a secondary feature, caused by glacial thrust from the south.

The sand layer (d) is well sorted, fine to medium grained and stratified. It contains some pebbly streaks. The pebble content is similar to that of the till (a), with an even higher amount of dolomite.

All the layers (b), (c) and (d) have a similarity in their lithologic composition with the underlying till (a). They are rich in dolomite in the −200 mesh fraction, (the ratio of calcite to dolomite: 0.1 to 0.3), with one exception: the calcareous gytta (c_4), where some calcite is of organic origin (produced by *Chara*). Similar ratios of calcite to dolomite in all the successive layers from the till (a) to sand (d) suggest that the principal source of the detrital material of the stratified drift in (b), (c) and (d) was the unweathered till (a). Another support for the derivation of (d) from (a) is their similarity in the pebble composition.

Lacustrine clay (e).—The next layer (e) is a stratified lacustrine clay without any distinct varving in the exposure, shown on figure 2. Varves are present in some of its portions closer towards Plum Point. Though the grain-size composition of the clays (e) and (b) is similar, they differ in their carbonate content: the ratio of calcite to dolomite of (e) is three times higher than in (b). This ratio is similar to that of the overlying tills (f_1) and (g). The lacustrine clay (e) was deposited in a lake that received muddy waters from the advancing glacier, which deposited the till (f_1) later on.

Clayey gravel (f_2) with reworked till (f_1) at its base.—This covers the folded layers of (a) to (d), except for a 60 foot long interval in figure 2. Here it has

TABLE 3

Mechanical composition, carbonate content of the −200 mesh fraction and till fabric Port Talbot interstadial site

Reference letter	File No.	Material			Mechanical composition (percentages)			Carbonate content in silt and clay fraction (less than .074 mm.) percentages				Local ice flow direction during deposition of till: average of several measurements along a one mile long exposure between Plum Point and Port Talbot
					sand	silt	clay	total	calc.	dol.	calc./dol.	
k	1176	lacustr. clay			11	55	34	34	18	16	1.1	
j	627	second bed of			17	36	47	33	16	17	.9	from ESE (pebble
j	380	"upper till"			39	48	13	33	16	17	.9	alignment)
i	1175	lacustr. clay			10	56	34	36	18	18	.8	
h	379	first bed of			12	29	59	32	16	16	1.0	from SE (striae on boulders along
h	421	"upper till"			27	28	45	32	16	16	1.0	the base of till)
g	459	"lower till"	+40 ft.	64	21	15	39	17	23	.7	from ESE (pebble
g	463		+33 ft.	68	18	14	38	17	21	.8	alignment)
g	462		+13 ft.	70	18	12	40	16	24	.7	from NE (pebble alignment)
g	461		+ 3 ft.	69	25	6	40	17	23	.7	from E (pebble alignment)
g	464		+ 1 ft.	62	21	17	37	17	20	.9	from SE (striae on
g	1161		+ 1 ft.	55	26	19	39	16	23	.7	boulder accumu-
g	1170		+ 1 ft.	66	22	12	38	13	25	.5	tions)
f_2	1169	dirty gravel			89	5	6	37	17	20	.8	
f_1	1168	till			47	21	32	38	18	20	.8	from S. (drag-folds, pebble alignment)
e	625	lac. top		5	39	56	41	15	26	.6	
e	624	clay base		8	23	69	40	16	24	.7	
d	1173	fine sand			88	12	0	35	9	26	.3	
c_6	623	silt top		14	74	12	50	6	44	.1	
c_6	622	silt middle		22	60	18	49	6	43	.1	
c_6	621	silt base		18	78	4	50	7	43	.2	
c_5	619	dark gyttja					14	2	12	.2	
c_4		light gyttja					24	9	15	.6	
c_3	618	silt			14	82	4	50	6	44	.1	
c_2	617	silt			16	81	3	49	6	43	.1	
c_1	1174	sandy silt			40	59	1	42	8	34	.2	
b	1166	varved clay			4	26	70	44	8	36	.2	
a	1165	till			60	26	14	43	7	36	.2	

been cut off by the overlying till (g). Most pebbles are subangular in the gravel (f₂). Voids between them are filled with clay, silt and sand; some pebbles seem to be wrapped in a clayey matrix.

This gravel was deposited by a very muddy water, or even by mud flows with a short-range transport. It is probably an ice-contact deposit. Similar inter-bedded gravel, cobble accumulations and till have been observed along the base of the "lower till" (g) and previously considered as its basal portion (Dreimanis and Reavely, 1953, p. 255). Lithologically, the layer (f) is similar to (g) (tables 2 and 3), but an erosional contact separates them (fig. 2). The till (f₁) is also more clayey than (g) at the gytta exposure. Occasional organic remains (see farther) have been found in both (f₁) and (f₂).

The till (f₁) has been deposited by an ice flow from the south (from the Lake Erie basin) as indicated by till fabric and ice-thrust deformations, particularly drag-folds in this till and underlying deposits, overturned towards the north. Most of these evidences have been gathered outside of the gyttja exposure, but some of the folds may also be seen in figure 2. The source of the till (f₁) will be discussed together with (g).

The olive gray sandy "lower till" (g).—This is the most prominent layer in the exposure studied. It is also interbedded with gravel, particularly near its base (below the dashed line in fig. 2). Accumulations of boulders, resembling boulder pavements, appear at several places in this basal portion. They are discon-tinuous, always *in* till and do not mark any subaerial surfaces. Their formation has been discussed in Dreimanis and Reavely (1953, p. 243–244).

Lithologically, the tills (g) and (f₁) are characterized by a high content of carbonates with a dominance of limestone, except for the −200 mesh, where the ratio of calcite to dolomite is around 0.7. The dolomite ratio to calcite increases with decrease of the grain-size, but not as much as in the lowermost till (a). The considerably lower amount of dolomite in the till matrix of (g) and (f₁) distinguishes them from the till (a). Occasional boulders of Precambrian tillites and marble have been found in this till (but not in the "upper tills").

The local ice-flow direction, deciphered from the till fabric and by statistical studies of striae on boulder accumulations in (g), has been first from SE, later on from E, then from NE and finally from ESE again. These changes in glacial movements have been gradual during the deposition of the basal till (g) (see table 3 for a summary; a detailed account on these directional studies will be given in a separate paper). Heavy mineral investigations (Dreimanis *et al.*, 1957, p. 160), together with the carbonate content in the till matrix, suggest that the regional movement of the glacier, which deposited the "lower tills" (g) and (f), was from north-northeast across the area north of Lake Ontario, missing most of the Ordo-vician dolomites between Ottawa and St. Lawrence.

Two layers of the "upper till" (h) and (j).—Each is followed by lacustrine clay (i) and (k) in the alphabetic order, and they fill the top portion of the exposure. All these four layers are pale brown and rich in clay and silt (except for sample No. 380, representing a reworked till). The pale brown colour probably is from the Queenston shale, picked up by the glacier at the base of the Niagara escarp-ment and crushed during transport. Occasional fragments of this reddish brown shale are found in the tills (h) and (j). The clay fraction of the gray tills (a), (f₁) and (g) is also brownish, indicating a common source of their matrix with the "upper till." As the "upper tills" are more clayey, the brown colour dominates in them more than in the sandy older tills. The total carbonate content in matrix of the "upper tills" is less than in the "lower," particularly because of a decrease in the amount of dolomite. The carbonate percentage is particularly low in the sand and pebble fractions.

Shale (mostly gray, some black) is the principal constituent of these coarser fractions and range as high as 63 percent. The gray calcareous and black non-

calcareous ·shales derive from the local Middle Devonian rocks in the Lake Erie depression. The dominance of local material results also in a very high ratio of Paleozoic to Precambrian rocks (6–19) in (h) and (j), much higher than in the older tills (1–5). A lower percentage of heavy minerals in the "upper till" (1.4 to 1.5 percent), if compared with the earlier tills (2.35 to 4.50 percent), is another proof of a lesser admixture of Precambrian material in the "upper tills."

The ratio of purple to red garnets is slightly higher in the "upper tills" (h) and (j) than in the lower ones (a), (f_1) and (g). According to Dreimanis *et al.* (1957), such a ratio, together with a high ratio of tremolite-actinolite to chlorite-serpentine, suggests a regional glacial movement from Labrador over the Grenville rocks northwest of Montreal, but avoiding the Ottawa-St. Lawrence dolomite area and moving probably west of it, as indicated by a relatively low amount of dolomite in till matrix. Local centres of glacial outflow may have existed in the Lake Ontario (Holmes, 1952, p. 1006) and Lake Erie Basins (Dreimanis and Reavely, 1953, p. 254), during deposition of the "upper tills," as suggested by a very strong erosion and outward transport of local rocks from these lake depressions.

The upper tills (h) and (j) contain also pebbles of lacustrine clays. They, together with the dominant clay and silt fraction of the till, must have been derived from preexisting clay deposits, younger than the lower sandy till.

Carbonate content of the lacustrine clay (i) is intermediate between the "lower till" (g) and the "upper till" (h, j). Apparently the melt-water streams from the glacier which deposited the "upper till" were not the only source of clay and silt; a considerable amount has been added from the reworked surface of the "lower till."

ORGANIC REMAINS

Ostracods.—Ostracods were found by Staplin (1953, pp. 86–88) in the layers c_3 to c_6 (Staplin's locality QW–31, samples A, B and C). The following species were determined by him: a) in c_6 (sample C)—*Candona ohioensis, Candona parachioensis* n. sp., (?)*Candona simpsoni, Cyclocypris forbesi, Limnocythere verrucosa, Cypridopsis vidua*; b) in c_4 (sample B)—*Limnocythere verrucosa* and fragments of other ostracods; c) in c_3 (sample A)—*Candona candida, Candona truncata, Candona simpsoni, Candona* spp., *Limnocythere trapeziformis* n. sp., *Limnocythere verrucosa, Cyclocypris ovum, Cyclocypris forbesi, Potamocypris variegata, Cypridopsis vidua.*

Staplin concludes from his findings, that "ostracods in the lower silt (c_3, A. D.) probably lived in the shallower weedy parts of the lake. A lowering of water level and the initiation of highly vegetated marsh conditions is indicated by the middle organic silt. Deepening of the water, at some later date, formed the upper layer (c_6, A. D.). *Candona ohioensis*, present only in the upper silt, now inhabits the Lake Erie's shallower parts. *Limnocythere trapeziformis* n. sp., abundant in the lower silt, is common in Mankato deposits of the Chicago region, occasional in the Sappa silt of Iowa, and unknown elswhere."

Molluscs.—Molluscs are common in the beds c_{2-6}. As the fragile shells have been crushed by glacial pressure, most of them disintegrated completely during removal from the compacted silt. A bulk sample of c_4 was sent to Dr. W. J. Wayne at the Geological Survey of the State of Indiana, but he experienced the same difficulties in extracting the shells. After having washed 20 pounds of silt, he succeeded only in recovering some specimens of *Valvata cf. V. lewisi Currier*, fragments of *Gyraulus*, probably *G. parvus*, both inhabitants of shallower water in the Great Lakes region and north of it, and a small species of *Pisidium* (personal communications).

Mastodon.—A well preserved middle portion of a tusk, one foot long and three inches in diameter, with sharply broken ends, was found in the clayey bouldery gravel (f_2) 600 feet north east of the N. E. end of section, shown on figure 2. Lack of any marks of glacial or stream abrasion suggest a very short transport.

Plant remains other than pollen grains.—Fruits and seeds were found abundantly in the gyttja layers c_4 and c_5. According to Dr. J. Terasmae, Geological Survey of Canada, most of them belong to Najas flexilis (Willd.) Rostk and Schmidt, with some Potamogeton gramineus L. and Menyanthes trifoliata var. minor Raf. Dr. H. Müller, from the Amt of Bodenforschung, Hannover, examined specimens, shown to him by Dr. W. J. Wayne. He found fruits and seeds of Najas cf. flexilis, Potamogeton cf. filiformis and Potamogeton cf. alpenis (personal communications). L. Staplin (1953, p. 87) mentions also "much Chara" in his sample B, equivalent to

TABLE 4

Length of bodies of Pinus sp. pollen grains, Port Talbot interstadial

	Total number counted	Number of pollen grains at an average body length of										
		26µ	30µ	34µ	38µ	42µ	46µ	50µ	54µ	58µ	62µ	66µ
Upper silt (C_6)	81	–		14		60		6		1		–
Gyttja (C_5)	39	–	–	3	7	23	3	3	–	–	–	–
Calcareous gyttja (C_4), upper ⅔	25	–	1	2	5	10	5	2	–	–	–	–
Calcareous gyttja (C_4), lower ⅓	32	–	1	2		7	7	5	7	5	1	–
Lower silt (C_3) 1 ft. below gyttja	45	–	–	6		18		5		10		6
Lower silt (C_2) 2 ft. below gyttja	83	1	3	6	20	24	17	8	4	–	–	–
Lower silt (C_2) 3 ft. below gyttja	69	–	1	6	9	31	14	4	2	1	1	–
Lower silt (C_2) 4 ft. below gyttja	41	–	1	5	15	15	3	2	–	–	–	–
Lower silt (C_2) 5 ft. below gyttja	51	–	1	4	11	22	13	–	–	–	–	–
Lower silt (C_2) 5¾ ft. below gyttja	41	–	1	2	14	21	3	–	–	–	–	–
Sandy silt (C_1) 7 ft. below gyttja	12	–	–	–	5	7	–	–	–	–	–	–

the lower portion of gyttja (c_4). All the above plants grow in shallow, mostly calcareous waters, either in the Lake Erie basin or farther north at present. A compressed fragment of spruce root (Picea sp., determined by the Forest Products Laboratories, Ottawa) was found in lacustrine clay (e) 1000 feet S. W. of the gyttja exposure. Unidentifiable megasocpic plant remains (compressed stems and fragments of leaves) were relatively abundant in the till (f_1) at the 270 foot mark of figure 2, and a splinter of Gymnosperm wood was found together with the

mastodon tusk in (f_2). Pieces of larch and spruce wood (*Larix* sp. and *Picea* sp., according to the Forest Products Laboratories) were discovered in the "lower till" (g) one mile S. W. of the gyttja exposure at Plum Point.

Pollen analysis.—This was applied in order to find out the climatic conditions prevailing during the depositions of the layer (c).

The ordinary KOH method was used for digestion of organic remains other than pollen grains. Carbonates were dissolved in dilute cold hydrochloric acid and silicates in cold hydrofluoric acid before applying KOH. Pollen grains were stained with basic fuxin and methilene blue. An average of 250 tree pollen grains was counted in each sample, except for the lowermost one, which rendered only 54 tree pollen grains.

Percentage of the non-tree pollen grains (NAP), including shrubs, like willow (*Salix*), was calculated by assuming the sum of the tree pollen grains as 100 percent. Most of the NAP were pollen of *Gramineae* (grasses).

The relative frequency of tree pollen grains in samples, or the so-called arboreal pollen frequency (APF) was determined arbitrarily: as the number of pollen grains per one 16 x 16 mm. slide. Such APF values are not suitable for comparison with results of other palynological studies, but they may give some idea on the frequency changes in this Port Talbot profile. Thus, the lowermost sandy
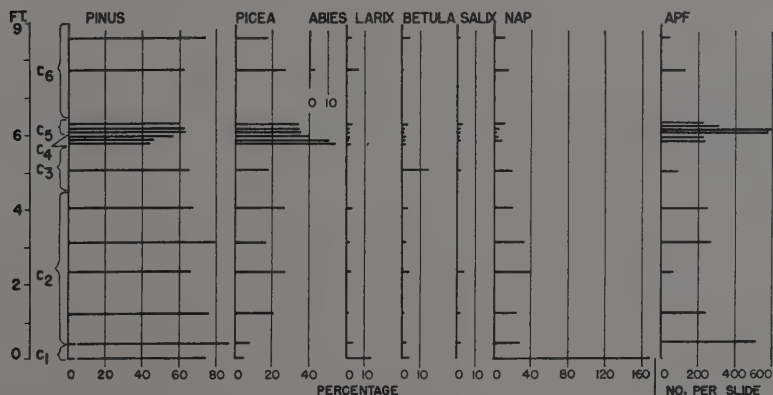
FIGURE 3. Pollen diagram of the Port Talbot interstadial section (c_1) to (c_6). NAP—non-arboreal pollen. APF—number of arboreal pollen grains per slide.

silt (c_1) has a much lower APF value (11) than other samples above it. NAP (168 percent) dominate over the tree pollen in the same sample. Both the low APF and high NAP values suggest that probably no forests existed along the northern shore of Lake Erie at that time. The tree pollen grains, found in this sample, may have been carried in by wind from the area south of Lake Erie.

The considerable variation of the APF values (42 to 620 percent, mostly over 200 percent, fig. 3) in other samples of the layer (c) may be due to the different characters of the sediments examined and various rates of admixtures of other organic remains. Thus, some samples rich in organic remains other than pollen have lower APF values. The low NAP percentage of the same samples (15 to 40) suggests a forest growth in the vicinity. This conclusion is supported also by a twig, found in (c_4).

Results of the pollen analysis (fig. 3) suggest that the following trees have grown along the north shore of Lake Erie during deposition of the layer (c): pine (*Pinus*

sp.), spruce (*Picea sp.*), larch (*Larix sp.*), birch (*Betula sp.*). Pollen grains of balsam fir (*Abies sp.*), elm (*Ulmus sp.*) and alder (*Alnus sp.*) were found to be less than 1 percent (except for 3 percent of fir in c_6), and their presence does not necessarily mean that the corresponding trees grew in vicinity. Wind transport from great distances or redeposition from older layers may be the explanation.

The length of the bodies of the pine pollen grains (between the outer points of the insertion of the bladders) was measured in nearly all slides (table 4). Results of these measurements group around two maxima: a) about $42\,\mu$ and b) 54 to $64\,\mu$. The smaller size ($42\,\mu$), which dominates through most of the section, compares well with jack-pine (*Pinus Banksiana* Lamb., length of the body 41 to $48\,\mu$) in Cain's (1940, p. 303) study of recent and fossil pollen grains. The larger pollen grains of pine, with bodies 54 to $64\,\mu$ long, are found particularly along the contact of the lower silt (c_3) and the calcareous gyttja (c_4). They may belong to the white pine (*Pinus strobus* L., bodies 55 to $60\,\mu$ long according to Cain) or the red pine (*Pinus resinosa* Ait., 55 to $64\,\mu$), common trees in the Great Lakes region.
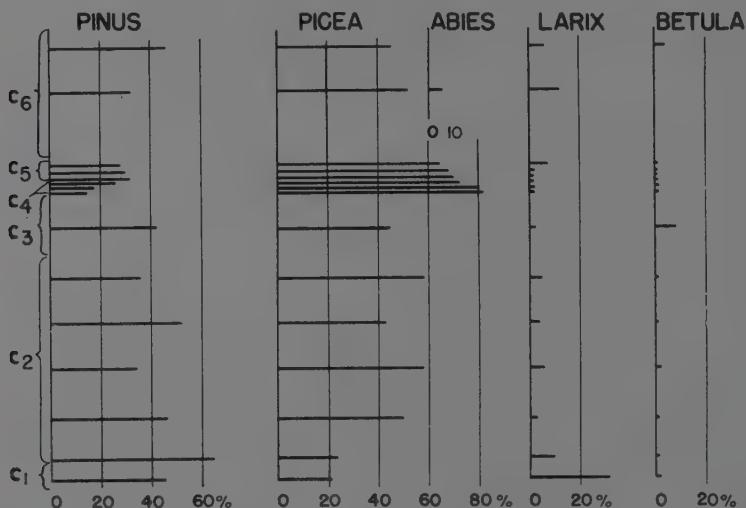
FIGURE 4.   Recalculated pollen diagram of the Port Talbot interstadial section, with the numbers of *Pinus* and *Betula* pollen grains reduced four times.

It is possible that the larger pollen grains of pine (54 to $64\,\mu$) include also other species of *Pinus* than *P. strobus* and *P. resinosa.*

Pollen grains of the same three species, measured by Deevey (1939, p. 696) are smaller: *Pinus Banksiana*:   28 to $56\,\mu$, mostly about $37\,\mu$; *Pinus strobus*: 41 to $55\,\mu$, mostly about $48\,\mu$; *Pinus resinosa*:   36 to $53\,\mu$, mostly 42 to $48\,\mu$. The relative size relationship between *P. Banksiana* and the other two species of pine remains the same. Differences in size measurements by Cain and Deevey may be caused by differences in treatment during the pollen analysis.

Pines and birches produce more pollen than most other trees, such as spruce. Therefore, the percentage of pollen grains of pine and birch have been reduced four times on figure 4, following suggestions by Faegri and Iversen (1950, pp. 87 - 88). That is done in order to obtain more adequate representation of the actual

composition of forests. The true association of forest trees was probably still different than that of the recalculated diagram, as we do not know the exact amount of productivity of various pollens. Another unknown factor is the percentage of poplar (*Populus sp.*), one of the most abundant recent forest trees in northern Canada, as its pollen grains do not preserve well.

The recalculated pollen diagram suggests a relatively equal abundance of pine and spruce during the deposition of the lower silt. A strong spruce maximum is at the base of gyttja (c_4) (immediately above the maximum of pines with the large pollen grains), and spruce still dominates through the gyttja and the upper silt, though gradually becoming less abundant. Pollen grains of larch (*Larix sp.*) are most abundant (10 to 12 percent) at the base of the lower silt and in the upper silt. Birch (*Betula sp.*) reaches its highest abundance (9 percent) in the silt one foot below the gyttja.

The Forest Research Division of the Department of Resources and Development at Ottawa was consulted regarding recent forests, similar to those represented by the pollen diagram of figure 3. Dr. J. D. B. Harrison, Chief of the Forest Research Division, answered that "extensive forests having a similar composition, with the exception of *Larix*, can be found today in the valleys around Gouin Reservoir at the headwaters of the St. Maurice River in Quebec." Climate of the Gouin reservoir area (48.5°N, 74°W) is with cold winters (January temperature slightly above zero) short, but relatively warm summers (mean July temperature 68°). The year has only 80 frost free days, as compared with 160 at the north shore of Lake Erie at present (Putnam, 1952, pp. 132–133, 222–223). Climatic conditions, similar to those described above, have probably existed along the north shore of Lake Erie during the deposition of most of the layer (c). Admixture of *Pinus* pollen grains belonging to another species than jack-pine (probably *P. resinosa* or *P. strobus*), at the end of deposition of the lower silt (c_3) suggest that the climate became slightly warmer at that time. The later decrease in size of *Pinus* pollens in the upper layer (c_{4-6}) indicates a cooling of the climate again.

Pollen grains were examined also in the till (f_1) – sample No. 1168, as it was rich in plant remains. The APF was found to be very low (20) and so also the NBP (30 percent). Pine dominated among the arboreal pollen (70 percent), with spruce and birch as the next most common trees (13 percent of each). The pollen grains of pine were of two sizes: a half of them with the length of body 40 to 48 μ, and the other half, 54 to 64 μ, the same as in layer (c). Except for one pollen grain, that looked like oak, and another of alder, all the other pollen grains were the same as in the layer (c). The two pollen grains of deciduous trees other than birch are not sufficient to conclude existence of warmer climatic conditions than represented by the interstadial layer (c). As no other tills separate the (c) from (f_1), a conclusion may be drawn that the secondary pollen grains in till (f_1) do not indicate any warmer climate during the preceding interstadial than suggested by the Port Talbot pollen diagram.

RADIOCARBON DATES

Samples of gyttja (c_5) and evergreen wood, found 1 mile S. W. from the gyttja exposure at Plum Point, have been submitted for C_{14} dating to various isotope laboratories. The first radiocarbon date of gyttja ($10,900 \pm 400$ yrs.), published in an abstract of a paper presented at the Geological Society of America meeting at Toronto (Dreimanis, 1953, p. 1414) later turned out to be erroneous.

Later C_{14} datings are listed in table 5.

Radiocarbon dates of the gyttja (c_5) represent only its minimum age, and the apparent variations in the figures are due to the instrumental range. If the oldest age is considered as the most reliable, the gyttja was deposited more than 39,000 years ago.

The three dates for the wood fragments, found in the lower till at Plum Point,

are at least 11,000 years younger. They range from $24,600 \pm 1600$ to approximately 28,000 years before present. The latest date may mean the approximate time of ice advance that deposited the "lower till" (g), and it agrees well with the age of the buried Cleveland wood: $24,600 \pm 800$ years (Suess, 1954, p. 469: W-71).

A question may arise as to what happened during the interval of more than 14,000 years between the deposition of the gyttja (c_5) and the till (g). Answers will be attempted on pp. 80–81.

It may be mentioned here that the time interval involving deposition of the "lower till" (g) and the first layer of the "upper till" (h) was less than 12,000 years. This figure is based upon the $24,600 \pm 1600$ years radiocarbon age of the spruce wood in the till (g) and the $12,600 \pm 440$ date of driftwood (McCallum, 1955, p. 34, sample No. S-25) from lacustrine spit gravels at Ridgetown, Ontario. This wood was found by Mr. A. Wade in 1954, 32 feet below the surface and immediately above the upper till, equivalent to (h). As the finder had kept the driftwood in a water barrel for a couple of weeks, contamination of the log by recent microorganisms was feared. Therefore, only the core of the log was sent for radiocarbon analysis. If the core were also contaminated, its C_{14} date may be

TABLE 5

Radiocarbon dates

Sample	C_{14} age	Laboratory Reference
Gyttja from the interstadial deposit near Port Talbot, Ontario, collected in Autumn 1951 (185A) and Autumn 1953 (W-100, S-7 and 217A)	greater than 32,000	U. S. Geological Survey, No. W-100, H. E. Suess, 1954, p. 471.
	greater than 25,000	Dept. of Chemistry, Univ. of Saskatchewan, No. S-7, K. J. McCallum, 1955, p. 34. Lamont Geological Observatory, W. Broecker, 1957.
	greater than 38,000	No. 185A
	greater than 39,000	No. 217A
Larchwood, from the "lower till" at Plum Point, Ontario collected in Autumn 1952, divided in two portions for C_{14} age determination	$28,200 \pm 1500$	Lamont Geological Observatory, No. 185B, W. Broecker, 1957.
	$27,500 \pm 1200$	U. S. Geological Survey, No. W-177, M. Rubin and H. E. Suess, 1955, p. 485.
Spruce wood, from the "lower till" at Plum Point, collected in Spring 1953	$24,600 \pm 1600$	Lamont Geological Observatory, No. 217B, W. Broecker, 1957.

slightly later than its actual age. Driftwood, collected by G. W. White at Cleveland, Ohio, from a "stratigraphic horizon between deposits of Lake Arkona and Lake Whittlesey," was dated $13,000 \pm 500$ years old (Suess, 1954, p. 469, No. W-33). If the possible contamination of the Ridgewood log is considered, it may be regarded as a Lake Arkona deposit. Without contamination it may be of an early Lake Whittlesey age.

STRATIGRAPHIC CORRELATIONS AND SEQUENCE OF EVENTS

It is not safe to base stratigraphic correlations upon one single Pleistocene exposure, like the one described in this paper. Therefore, the writer has also used results of studies of Pleistocene deposits elsewhere in Southern Ontario for crosschecking, even if they have not been described in this paper.

The following sequence of events is proposed by this comparative study, with

an emphasis on the Port Talbot and Plum Point sections (see also Dreimanis, 1957, pp. 166–168):

1) Advance of an ice lobe either a) from north east along the St. Lawrence lowlands, Lake Ontario and Erie or b) from the north via Georgian Bay, and deposition of the till layer (a). The "early" Wisconsin tills, which underlie the buried soil at Sidney, Gahanna, and other places in Ohio (Goldthwait, 1957; Forsyth and LaRocque, 1956, p. 1696), were deposited probably during the same subage. This glacial advance is correlated with the yet unnamed early Wisconsin glaciation, concluded by Flint and Rubin (1955, p. 9), and Goldthwait (1957) from radiocarbon dates. Flint (1956, p. 285) calls it also a post-Sangamon and pre-Wisconsin glaciation. It seems to correspond to the early Würm subage in Europe (Woldstedt, 1956, p. 84) and may be called the Early Wisconsin here.

2) When the early Wisconsin glacier retreated towards the north-east end of Lake Erie, its basin became occupied by a proglacial lake. The lake level was higher than at present, because the eastern outlet across the Niagara escarpment was blocked by the glacial ice. The varved clay (b) was deposited in this lake.

3) Further retreat of the glacier towards the north-east opened a lower outlet for the Lake Erie depression, comparable to the present Niagara gorge.

The buried St. David's channel (Spencer, 1907, pp. 133) which trends from Whirlpool of the present Niagara gorge towards north west may have been formed during this interstadial. Wood of white spruce has been reported by Spencer (pp. 133–134) 186 feet deep in the drift that fills the St. David's gorge. White spruce is considered to be one of the most northerly growing trees in Canada and fits well in the climatic conditions of the Port Talbot interstadial. The lake level was first lower than the present one, as the surface of the Niagara peninsula had been depressed by the glacial load, and the rise of land was slow and gradual after retreat of the glacier. The lower silt (c_1–c_3) and gyttja (c_4–c_5) were deposited in shallow near-shore waters of this predecessor of Lake Erie or in a small lake marginal to Lake Erie. The original position of the layers (c_1) to (c_5) must have been below the present lake level, as they have been folded above it by a later glacial thrust.

No forests bordered the north shore of Lake Erie at the beginning of (c_1), but spruce, jack-pine, larch and birch began to grow soon. As the climate improved, pines with larger pollen grains (probably red and white pine) immigrated at the end of deposition of the silt (c_3), disappearing however soon again. The transitional zone from (c_3) to (c_4) with the spruce maximum and presence of pines also other than *Pinus Banksiana* is considered as the thermal maximum of the interval between deposition of the tills (a) and (f_1). This thermal maximum was cooler than the present climate along Lake Erie. Therefore, the term *interstadial* rather than interglacial seems to be appropriate for this interval.

A similar but more extensive peat layer with plant remains indicating cold, moist climate and freshwater environment have been found in the St. Lawrence lowlands at St. Pierre, Quebec, between Montreal and Quebec City (Gadd, 1953, p. 1426). The radiocarbon date ($11,050 \pm 400$) mentioned in the above paper, turned out to be erroneous. The later determinations (Rubin and Suess, 1955, p. 485: W–189; Preston *et al.*, 1955, p. 958: Y–242, Y–254, Y–255, Y–256) of this and other peat beds in the vicinity gave much greater ages: $> 30,000$ or $> 40,000$.

A cold climate peat ball in gravel, with pollen grains of spruce and pine, older than 34,000 years (W–194), has been found at Amber, near Toronto, Ontario (Dreimanis and Terasmae, 1956, pp. 8–9 and 20–21). Matrix of the underlying till is also richer in dolomite than the two tills above the gravel, suggesting that it was deposited by an ice flow from northeast across the Ordovician dolomite area (p. 9). This dolomitic till may be correlated with till (a) of Port Talbot.

If all the above cold climate peats belong to the same interstadial as the Port Talbot gyttja, the lake Ontario basin and the St. Lawrence lowlands were

not covered by a glacier at that time. How far the ice-sheet retreated in Labrador is still unknown.

As the maximum of the Port Talbot interstadial was more than 39,000 years ago, more elaborate methods of radiocarbon datings and other isotope studies have to be applied in the future for finding a closer absolute date. Some of the recent studies on climatic indications and ages of extraglacial ocean and lake deposits (Hough, 1953; Suess, 1956; Ericson *et al.*, 1956; Clisby and Sears, 1956) suggest that the above cool and relatively long interstadial interval may have existed approximately 45,000 or even 70,000 years ago.

Duration of the interstadial time may be inferred from the depth of leaching in buried soils of this interval. Flint and Rubin (1955, p. 652) have concluded that the 48 inch leaching at Sidney, Ohio, represented 16,000 years. Goldthwait (1957) arrives at even smaller figures: 5 to 15 thousand years. The available radiocarbon dates permit a longer interval.

Many evidences have been gathered in Central and Western Europe on a similar long and moderately warm interstadial, that separated the early Würm or Würm I from the main or middle-Würm (Woldstedt, 1956, pp. 82–83). As the climate of this interstadial was temperate and not cold, some authors have considered it as an interglacial (see Zeuner, 1954; and Gross, 1956, pp. 87–101 for a detailed discussion). Gross (1956, p. 97) estimates that this so-called Göttweig interstadial had lasted for approximately 15,000 years, ending 23,000 radiocarbon years ago. There are some other radiocarbon dates from Belgium (a peat lens at Godarville, older than 36,000 years, according to Rubin and Suess, W–173: 1955, p. 486) and in Holland (North East Polder, Nos. 530–534 Gröningen: from 39,200 ±1500 to more than 55,700 years, according to DeVries *et al.*, 1956) that suggest an earlier beginning of the interstadial than 23,000+15,000 years ago. It should be mentioned that the North East Polder peat is generally considered as belonging to the Eemian (= Sangamon) interglacial, but its relatively late radiocarbon ages suggest that it was deposited during an early Würm (= Wisconsin) interstadial.

4) Accumulation of gyttja was interrupted by deposition of the upper silt (c_6), and sand was laid down on the silt, probably by a lake current. These are indications of a rise of water, that may have been caused by a gradual uplift of land in the Niagara outlet area. Spruce decreased and jack-pine increased in abundance in the nearby forests.

5) The lake level rose considerably during the deposition of the lacustrine clay (c), because of blocking of the lake outlet by an advancing glacier. Muddy waters from the glacier were the principal source of the clay and silt of (c).

6) The glacial lobe that entered the Lake Erie depression from the north east spread out radially from the lake bed, thus overriding the north shore from the south and depositing the till (f_1). This glacial advance terminated the long interstadial which had its thermal maximum more than 39,000 years ago. What concerns the time of this advance, the writer considers two possibilities:

a) One of them is that deposition of till (f_1) initiated a long lasting major glaciation (see also Flint and Rubin, 1955, p. 657), beginning approximately 25,000 years ago in the Lake Erie area. In such a case (f) is merely the basal member of the "lower till" (g) and the unconformity between (f) and (g) has been caused by change in glacial movement or local oscillations.

b) Another possibility is that deposition of till (f_1) was much earlier than 25,000 years ago. It represented an ice advance separating the Port Talbot interstadial (>39,000 years old) from another ice-free interval. This hypothesis is suggested by the more than 12,000 years wide gap between the "old group" and the "middle group" radiocarbon dates (Flint and Rubin, 1955, pp. 657–658) including the new Plum Point date of 28,000 years, by absence of any "middle group" dates in the area north or north-east of Southwestern Ontario, and because of finding the Plum Point wood not in the till (f_1), but in the next higher layer (g). If this

hypothesis is correct, the Main Wisconsin glaciation began to affect the Great Lakes region considerably earlier than 25,000 years ago. Its first advance which deposited the till (f_1) may have not reached south beyond Lake Erie, and it was probably short, followed soon by a retreat towards the north east. Evergreen forests returned in the Lake Erie region, at least 28,000 years ago or probably before that, but absence of similar evidences from the areas north of Lake Ontario and in St. Lawrence lowlands suggests that the ice may have remained there or at least in the vicinity. The lake shore in the Erie depression must have been farther south than at present, as the larch and spruce wood, found in till (g), has been transported from south east. The short above glacial advance into the Lake Erie basin may have had little influence on the climate farther south of Great Lakes, and an uninterrupted long interstadial interval existed there, terminating 25,000 years ago, or even later.

More facts, particularly radiocarbon dates are needed to check whether the hypothesis (b) is tenable.

7) A continuous long glacial cover existed over the north shore of Lake Erie since burial of the 25,000 year old forests, while depositing till (g). The glacial movement was first along the Lake Erie depression, and the ice lobe spread out of it towards the surrounding land. Later on, probably with increase of the thickness of the ice, during the maximum of the Main Wisconsin glaciation, the glacial movement was from NE in the Port Talbot area: it came right across the land disregarding the topographic differences of lake depressions and the higher ground between them. Till was deposited continuously during these changes of the ice-movement in Southwestern Ontario. Similarities in till lithology from the bottom to the top of the till (g) indicate a relatively constant regional ice-flow: it was from N. E. towards S. W. Towards the end of deposition of till (g) the local ice movement was from S. E. again along the north shore of Lake Erie. The ice sheet had become thinner, and it resumed a lobate character, flowing principally along the major depressions. This was a sign of retreat of the glacier.

8) The Erie lobe retreated at least as far as the eastern portion of Lake Erie, as indicated by the regionally persistent textural and lithologic differences between the "lower till" (g) and the "upper till" (h) not only in Southwestern Ontario, but also in Northern Ohio (White, 1951, p. 971; and Shepps, 1953, pp. 43–45). The upper till is considerably more clayey than the lower one, and it is thicker than 100 feet in many places. Such large masses of clayey till must have been formed by reworking of extensive lacustrine deposits that covered the lower till and still cover it in some places. Since the retreat of the Erie lobe for a couple of hundred miles and the following readvance for the same distance, measured along the axis of the lake, required several thousands of years, this oscillation may be considered as an interstadial subage, at least for the Lake Erie region, and therefore called here the *Erie interstadial*. Further studies are still necessary to determine how far and when did the ice retreat, and how this retreat correlates with other areas in the Great Lakes region.

9) The already mentioned clayey "upper till" was deposited by that glacial advance which reached beyond the Defiance moraine farther south west (White, 1951, p. 971). When the Erie lobe retreated, proglacial lacustrine deposits, such as (i) and (k) at Port Talbot, were laid down in front of it in the Erie basin. Several layers of the "upper till" were deposited in areas where the glacial margin oscillated, for instance (h) and (j) at Port Talbot. The layer (j) terminates one mile west of the gyttja exposure, but it may be traced for at least 20 miles towards the east. It seems to correspond to the oscillation that formed the Tillsonburg moraine. All these glacial oscillations and lacustrine activities occurred during the development of the following lake stages in the Erie basin: 1) Lake Maumee, 2) Lake Arkona, 3) Lake Whittlesey and 4) Lake Warren. The top of the Port Talbot exposure (675 feet above sea level) was below the water level of all the above lake stages.

The sequence of glacial and interstadial subages, as postulated by the writer for the north-central portion of Lake Erie basin, is summarized in table 6, together with the index letters of layers, exposed at Port Talbot.   This is not considered as a complete and well-proven stratigraphic sequence, but merely a suggestion, open for criticism and comparison with other late Pleistocene stratigraphies of the adjoining areas.   Therefore, temporary local terms are used for the substages until it is possible to correlate them with generally accepted stratigraphic names.   We are at a stage of re-evaluation of Pleistocene stratigraphy, and every report of progress with certain working hypotheses will assist in building up a more correct stratigraphy of the Pleistocene.

TABLE 6

Proposed Wisconsin stratigraphy for the north shore of Lake Erie, central portion

Number of glacial cover*	Glacial and Interstadial Subages; important events in the Lake Erie basin	Index letters and types of deposits or unconformities at Port Talbot
IV	*Main Wisconsin glaciation* *Final glacial advance*, and the Maumee, Arkona, Whittlesey and Warren stages of proglacial lakes during the oscillatory retreat of ice towards the north east. *Erie interstadial:*	lacustrine clay (k) till (j) lacustrine clay (i) till (h)
	Retreat of the Erie glacial lobe towards the eastern portion of Lake Erie, followed by a proglacial lake.	unconformity (lacustrine deposits elsewhere)
III	A long-lasting uninterrupted *glacial cover*, but with changing directions of ice movements.	till (g)
	Plum Point *interstadial* wood (reworked) approximately 25,600–28,000 years old.	erosion, unconformity
II	*Glacial advance* from northeast down to the Lake Erie depression, probably beginning the main Wisconsin glaciation. *Port Talbot interstadial*	till and gravel (f) lacustrine clay (e)
	Ice sheet retreats far north. Cool temperate climate with evergreen forests. Thermal maximum more than 39,000 years ago.	sand (d) silt and gyttja (c)
I	*Early Wisconsin glacial subage* Extensive glacial cover, followed by a proglacial lake.	varved clay (b) till (a)

*The tills underneath the lake level, representing older glacial advances of unknown age, are not included here.

APPENDIX

While discussing age of the layer (f), the author did not have any radiocarbon dates for crosschecking the assumed alternatives of approximately 25,000 years or

considerably more than 25,000 years (see p. 80). Thanks to the excellent co-operation of K. J. McCallum at the radiocarbon laboratory of the University of Saskatchewan, a splinter of conifer wood, found together with a fragment of a mastodon tusk (see p. 73) was dated recently. Its age was determined to be more than 34,000 radiocarbon years (S–46). The fresh appearance of wood suggests that it was not picked up by glacier from a peat deposit, but most probably derived from a forest, overwhelmed by the glacial advance. Though reworking of old glacial drift is not excluded, lack of abrasion marks on both the wood and the tusk suggest more probably that their age does not differ much from the age of the glacial advance, which deposited the till (f_1). If so, till (f_1) is more than 34,000 years old (see the alternative (b), p. 80), and it represents a glacial advance separating the Plum Point interstadial from the Port Talbot interstadial (table 6). Another radiocarbon date is anticipated on the (S–46) material as a cross-check.

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SOME EFFECTS OF DIETARY PENICILLIN ON THE GERMAN COCKROACH, *BLATTELLA GERMANICA* (L.)[1]

(ORTHOPTERA: BLATTIDAE)

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Although considerable information has appeared in the literature relative to the effects of the addition of small amounts of antibiotics to the diets of vertebrates, especially domesticated animals, comparatively little has been reported concerning the effects of these antibiotics on insects.

Working with aureomycin, Brooks and Richards (1955) obtained bacteroid free nymphs of the German cockroach by feeding their parents a dog food diet containing 1,000 ppm. of the antibiotic all of their lives. The bacteroids were not eliminated from the parents, but were absent from their offspring. The aposymbiotic (without intracellular bacteroids) nymphs thus produced were practically incapable of growth on a natural diet which was adequate for nymphs containing bacteroids. Higher concentrations of aureomycin resulted in excessive mortality.

De (1956) reported that streptomycin administered in the diet of stored grain beetles at 200 to 1,000 ppm. had no apparent effect on the insects. If anything, it extended the length of life. Steinhaus and Bell (1953), in attempting to obtain intracellular bacteroid free stored grain beetles by adding antibiotics to the grain, found chloromycetin, penicillin G, polymixin B, streptomycin, and terramycin to be highly toxic. At levels of 20,000 to 36,000 ppm., 100 percent of the beetles were dead in 30 to 60 days. Mengle and Fisk (1956) fed adult female German cockroaches high concentrations of 11 antibiotics, five of which produced little or

no mortality even at 20 percent of the weight of the diet. The other six produced significant mortality when fed at the same level.

The work reported herein concerns some effects of the oral administration of fifteen different dietary concentrations (6 to 100,000 ppm.) of crystalline sodium penicillin G (Sharpe and Dohme) to the German cockroach. Starting with six parts per million, the penicillin concentration of each succeeding dietary level increased geometrically by a factor of two.

MATERIALS AND METHODS

The cockroaches used were from a normal (non-insecticide-resistant) strain which had been reared for several years on pulverized Purina dog checkers in the insect rearing room of The Ohio State University.

To obtain first instar nymphs for the dietary studies, approximately 30 capsulated female cockroaches were placed in each of two five gallon glass jars. The top two inches of each jar were coated on the inner surface with a mixture of petroleum jelly and mineral oil to prevent escape of the females and their offspring. In addition, the jars were securely covered with two layers of cheese cloth to prevent escape or contamination with other cockroaches. All other rearing chambers used in these experiments were similarly greased and covered.

The capsulated females in the five gallon jars received distilled water from a large vial plugged with absorbent cotton and a diet consisting of equal parts of vitamin free casein, dextrose, and powdered non-nutritive cellulose. The first instar nymphs received no other nutrients until placed on the test diets.

The following procedure was used for handling the first instar nymphs: 1) In three or four days, when most of the eggs from the capsulated females had hatched, the jars were placed in a deep freeze until the cockroaches were inactive. 2) The young were then removed by use of a wet camel's hair brush and groups of approximately 35 were placed in individual pyrex crystallizing dishes, five and three-fourths inches in diameter and three inches deep. 3) A few hours later, the cockroaches were again chilled and each group was weighed and reduced to 30 individuals in order to provide groups of cockroaches uniform as to initial weight. 4) Distilled water in a vial three inches by one inch in diameter, plugged with absorbent cotton and one of the prepared diets in a vial two inches by one and one-half inches in diameter were added to each dish. 5) The dishes were placed in a constant temperature-humidity box set at $27 \pm 1°C$ and approximately 73 percent relative humidity. The humidity was controlled by placing two three quart capacity jars filled with saturated sodium chloride solution into the cabinet. Water was added to the jars as necessary. The insects were kept in the dark except when subsequent weekly weighings were made.

All weighings were performed with a Roller-Smith Torsion Balance graduated from 1 to 1,500 milligrams. The cockroaches were picked up individually by the antennae with a fine forceps and placed on the weighing pan. Weighings were made at weekly intervals from the first instar to the adult stage. For all but the initial weighing, the insects were anesthetized with carbon dioxide. New food and water were added weekly.

Cockroaches, even from the same egg capsule and reared under apparently identical conditions, reach the adult stage in different lengths of time. Because recordings of the weights of replicates containing both nymphs and adults would be of little value in determining the growth rate during the developmental period, it was necessary to designate a particular point as the "adult stage." Therefore, when 10 percent of the individuals in a test had actually reached the adult stage, or when the average weight per roach exceeded 42 mg., the whole group was considered to have reached the "adult stage." In following this procedure, it was found that approximately 40 to 50 percent of the insects would actually reach the adult stage in the following week.

The basic diet used throughout the study was micromixed pulverized "Purina Dog Chow Checkers," manufactured by the Ralston Purina Company of St. Louis, Missouri.

Sixteen diets were prepared, fifteen of which contained a different concentration of penicillin.   The preparation of the diets was as follows: 1) Approximately 500 grams of the dog food were placed in a large beaker and mixed thoroughly; 2) For each diet a definite quantity of the dog food was weighed and placed into a small, wide mouth bottle to which was also added a small but definite quantity of Alphacel (powdered, non-nutritive cellulose) purchased from the Nutritional Biochemical Corporation, Cleveland, Ohio; 3) The appropriate quantity of sodium penicillin G was dissolved in five milliliters of water and added to each diet.   Dilutions of a stock solution were used in the small concentrations for greater accuracy and convenience; 4) After the addition of penicillin, each diet was mixed thoroughly and dried in a vacuum oven at room temperature for 24 hours (table 1); 5) After drying, each of the various diets was again throughly mixed by grinding in a mortar and pestle.   The prepared diets were stored in a deep freeze until needed.

TABLE 1

Composition of the diets employed in the rearing experiments

Diet No.	Grams Dog Food	Grams Alphacel	Grams Penicillin*	Ppm. Pen./Diet	Grams Total
1 (ck)	18.0	2.000	0.000000	0	20.000
2	18.0	2.000	0.000122	6	20.000
3	18.0	2.000	0.000244	12	20.000
4	18.0	2.000	0.000488	25	20.000
5	18.0	2.000	0.000976	50	20.001
6	18.0	1.990	0.001953	100	19.991
7	18.0	1.990	0.003906	195	19.994
8	18.0	1.990	0.007812	390	19.998
9	18.0	1.980	0.015625	781	19.995
10	18.0	1.968	0.031250	1562	19.999
11	18.0	1.938	0.062500	3125	20.000
12	18.0	1.875	0.125000	6250	20.000
13	18.0	1.750	0.250000	12500	20.000
14	18.0	1.500	0.500000	25000	20.000
15	18.0	1.000	1.000000	50000	20.000
16	18.0	0.000	2.000000	100000	20.000

*Dissolved in 5 ml. of H_2O by appropriate dilution of stock solution.

RESULTS AND DISCUSSION OF FIRST GENERATION STUDIES

As outlined above, for the first generation studies, fifteen diets containing different quantities of penicillin plus a check containing no penicillin were prepared.   Two replicates of 30 German cockroaches each were set up on each test diet.   The insects were weighed each week from the initial weighing to the adult stage.   The results of this experiment, in average weight in milligrams per cockroach per week, are recorded in table 2.

Figure 1 indicates that between the fourth and fifth weeks of rearing there was a beginning of inhibition of growth in the cockroaches fed diets containing the higher levels of penicillin.   Figure 1 also represents the differences in weight at nine weeks.   At this time, the cockroaches reared on the check diet reached the adult stage.

An analysis of variance was used to estimate whether the rates of gain produced by all the treatments were equal or unequal (table 3).   The results of the test indicated that the growth rates were not equal.

The differences between the individual treatments and the check were then tested for significance by the method of Least Significant Difference (L.S.D.). Difference was not encountered with diets 2 to 8, but was encountered with diets 9 to 16.

Therefore, growth rates of cockroaches reared on the test diets appeared to be equivalent to the check diet if the diets did not contain more than 400 ppm. of penicillin.   However, this inhibitory trend did not become noticeable until the fifth week, even in the highest dietary levels.   This seems important because the growth rate was more rapid (logarithmic) during the first four week period.   The cockroaches almost doubled their weights from the initial weighing to the first week and also from the first to the second week.   Since no inhibition was apparent
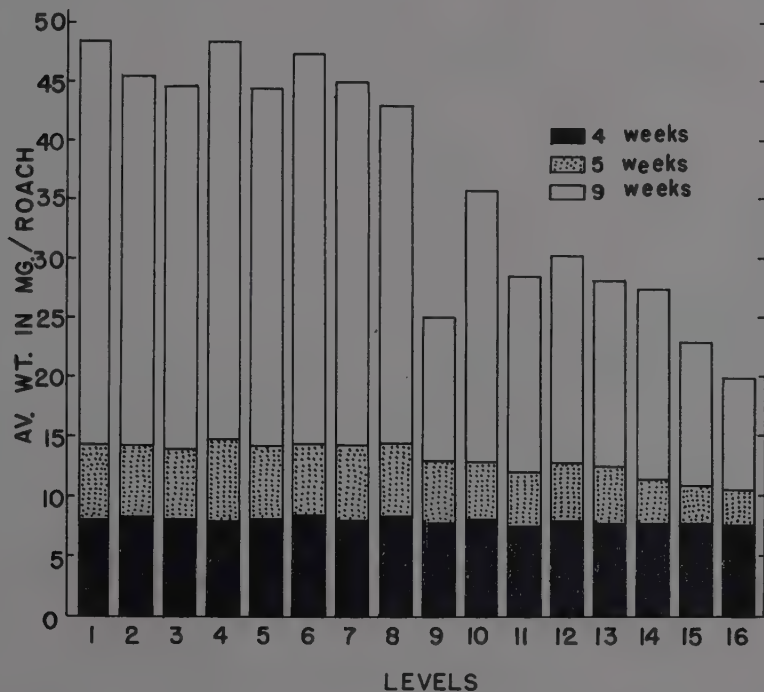
FIGURE 1.   Growth of the German cockroach at four, five, and nine weeks, when reared on diets containing different concentrations of penicillin.

during these first weeks, the effect or effects of penicillin were latent or non existant at this time.   Perhaps the penicillin inhibited the further accumulation or elaboration of some essential substance present in the nymphs at hatching.   If this could occur, inhibition of growth would not be apparent until the supply of the unknown substance, present in the nymphs at hatching was exhausted.   This supposition is somewhat substantiated by the fact that inhibition was evident earlier in the second generation where it was first observed between the second and fourth weeks.

It is possible that inhibition, particularly at higher levels, could have arisen through reduction of the intracellular bacteroids of the cockroaches.   Brooks and

Richards (1955) found that 1,000 ppm. of aureomycin did not eliminate the bacteroids from the cockroaches. Higher levels eliminated the bacteroids, but also resulted in excessive mortality in three or four months time. However, since no such excessive mortality occurred in first generation cockroaches fed diets containing as much as 100,000 ppm. of penicillin, it is possible that this

TABLE 2

Weights of first generation roaches on test diets

Diet Number					Avg. Wt. in Mg./Roach Week						
	Initial	1	2	3	4	5	6	7	8	9
1 (check)	1.37*	2.59	4.78	7.19	8.01	14.27	20.68	26.47	41.47	48.52
2	1.33	2.56	4.78	6.88	8.24	14.20	20.24	25.94	39.17	45.63
3	1.32	2.47	4.67	6.80	8.01	13.83	19.07	25.86	37.81	44.07
4	1.34	2.46	4.72	7.53	7.88	14.56	19.50	27.01	43.27	48.23
5	1.35	2.62	4.60	7.07	7.96	13.78	18.92	27.92	31.52	43.53
6	1.34	2.61	4.75	7.07	8.32	14.33	20.01	26.09	39.62	46.77
7	1.33	2.43	4.47	6.70	7.75	13.90	18.57	26.34	38.67	45.03
8	1.33	2.43	4.56	7.18	8.35	14.31	19.18	26.29	38.70	42.71
9	1.37	2.62	4.44	6.82	7.62	13.15	17.52	23.77	20.45	25.03
10	1.32	2.44	4.70	6.52	7.89	13.26	15.82	22.78	30.78	35.70
11	1.33	2.38	4.25	6.44	7.20	11.86	13.82	18.34	24.35	28.01
12	1.33	2.47	4.55	6.64	7.68	12.80	14.56	19.74	26.60	30.18
13	1.33	2.66	4.24	7.00	7.79	12.40	14.49	19.92	25.46	28.61
14	1.34	2.45	4.53	6.31	7.60	11.61	13.59	19.16	22.62	26.92
15	1.37	2.44	4.42	6.20	7.54	11.03	12.64	18.28	19.71	23.01
16	1.39	2.64	4.17	6.20	7.14	10.36	11.36	14.92	17.00	19.58

*The two replicates of approximately 30 insects each agreed well as to total weight, and only the average of the two is recorded. Complete data are on file in the editor's office or may be obtained from the author upon request.

TABLE 2 continued

Weights of first generation roaches on test diets

Diet Number	Avg. Wt. in Mg./Roach Week							
	10	11	12	13	14	15	16	17
1 (check)	——§	——	——	——	——	——	——	——
2	——	——	——	——	——	——	——	——
3	——	——	——	——	——	——	——	——
4	——	——	——	——	——	——	——	——
5	——	——	——	——	——	——	——	——
6	——	——	——	——	——	——	——	——
7	——	——	——	——	——	——	——	——
8	——	——	——	——	——	——	——	——
9	37.08	52.00	——	——	——	——	——	——
10	41.62	46.43	——	——	——	——	——	——
11	33.72	38.75	——	——	——	——	——	——
12	35.70	40.26	——	——	——	——	——	——
13	32.80	36.76	——	——	——	——	——	——
14	31.21	33.00	38.76	44.05	——	——	——	——
15	27.38	30.82	34.70	42.50	——	——	——	——
16	20.60	23.30	26.28	30.00	33.36	35.56	36.00	37.50

§No records because the cockroaches had reached the adult stage.

antibiotic did not affect or completely eliminate the bacteroids. The possibility also exists that penicillin is much less toxic to cockroaches than is aureomycin, and the excessive mortality associated with high concentration of aureomycin was due to its direct toxic action on the insect.

First generation cockroaches receiving less than 780 ppm. of penicillin reached the adult stage at approximately the same time (fig. 2). This is well correlated with the estimate that the growth rates were statistically equivalent. In the levels containing 780 ppm. or more, however, there was an inverse relationship between time to adult stage and growth rate. The cockroaches on all diets in both generations molted to the true adult stage at approximately the same weight. Thus, smaller adults did not result from higher penicillin concentrations. It merely took them a longer time to achieve the normal size and weight for the molt to the adult stage.

Anorexia did not appear to be a problem in the various dietary levels with the possible exception of diet 16 (100,000 ppm. of penicillin). If the phenomenon
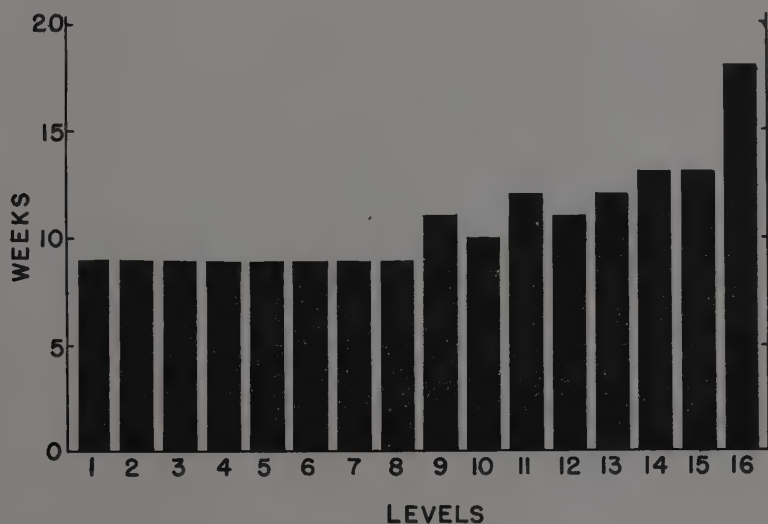
FIGURE 2. Time in which the German cockroach reached the adult stage, when reared on diets containing different concentrations of penicillin.

actually occurred, it was not evident until after the fourth week, because, even on diet 16, growth was almost as great as the check up to that point. The cockroaches did not appear to be repelled by the penicillin in any way.

The reviews of Jukes and Williams (1953), Stokstad (1954), and Jukes (1955) contain numerous references pertaining to the acceleration of growth in vertebrate animals, incited by the addition of small quantities of antibiotics in the food. In general, the antibiotics were added at about 10 ppm., and the extent to which it is absorbed by the animals at this low level is questionable. Most evidence to date indicates that the antibiotic exerts its action primarily on the intestinal biota.

No acceleration of growth was observed in this study. Had the cockroaches been reared under unsanitary conditions, or on a diet deficient in protein or vitamins, the results might have been different. In vertebrates reared in clean

quarters or under aseptic conditions, growth increases usually do not occur with antibiotic fortified feeds (Luckey *et al.*, 1956).

The mortality in the various levels in the first generation was generally low. There appeared to be little difference in mortality in the various treatments with the exception of diet 9. The high mortality with diet 9 (36 percent), however, cannot be satisfactorily explained. There is a good possibility that these insects became diseased early in the course of the test. Disregarding diet 9, the mortality varied between 3.7 and 11.9 percent, which is considered quite low in view of the fact that the insects were handled and anesthetized once each week from the time of hatching to the adult stage. However, Steinhaus and Bell (1953) found that 20,000 to 35,000 ppm. of penicillin added to grain killed one hundred percent of the two species of stored grain beetles tested, over a period of 30 to 60 days.

Reproduction by the first generation appeared to be decreased by all test diets containing 200 or more ppm. of penicillin (diets 7 to 16). This reduction was estimated to be about 40 to 50 percent at 200 ppm. (diet 7), and increased to about 99 percent at 50,000 ppm. (diet 15) and 100 percent at 100,000 ppm. (diet 16), where no egg capsules were produced. The egg capsules produced by the females at these levels were generally smaller than normal, and commonly misshapen. Many egg capsules were dropped prematurely, with none of the eggs hatching. In addition to being shriveled, some of the capsules were blackened and the embryos inside were dead. Figure 3 illustrates several of the deformed egg capsules compared with normal ones.

TABLE 3

Analysis of variance of the growth rates with the sixteen diets

Source	SS	DF	MS	F	F-5%	F-1%
Treatments	.3758	15	.02505	9.1221*	2.35	3.41
Error	.0209	16	.00131			
Total	.3967	31				

*Significant at 1% level.

Growth time equals the entire growth period. Test based on two replications of 30 cockroaches each, per treatment.

Since very few young were produced at the higher levels of penicillin concentration, and no egg capsules were formed at the highest level (100,000 ppm.), there is a good possibility that the ovaries of the females were impared from functioning normally. Brooks and Richards (1955) found 5,000 ppm. of aureomycin produced this effect with the German cockroach in 90 days. Glaser (1946) reported the same results with calcium and sodium penicillin on the American cockroach.

MATERIALS AND METHODS IN SECOND GENERATION STUDIES

In preparing tests for the second generation studies, three principal difficulties were encountered: 1) the first generation female cockroaches reared on any particular test diet matured at different times and therefore produced egg capsules at different times; 2) the egg capsules produced by these females contained varying numbers of viable embryos; 3) as a result of the foregoing, the numbers of second generation first instar nymphs of the same age available at any given time in any particular diet group was limited. This influenced the number and replications of some (diet levels 8 to 15) second generation tests.

The offspring from each first generation diet, where available, were reared on both the control diet and the diet of their respective parents. It was desired to have two replicates reared on these two diets, but in some cases, it was not possible

to obtain enough suitable insects for two replicates per diet.   In such cases, only one was employed.

First instar nymphal cockroaches for the second generation studies were obtained as follows.   The cockroaches which reached the adult stage on the test diets were allowed to mate and produce egg capsules, if any.   Then first generation female cockroaches with darkly pigmented egg capsules were removed as they became available in each test group.   The dark pigmentation indicated that the eggs would soon hatch.   Two to four such females from each diet were placed in each of four clean crystallizing dishes, two containing the check diet and two containing the respective parental diet on which the young were to be reared.

When the eggs hatched, the adult females were removed, and the number of offspring in any one dish was reduced to thirty.   The initial weights of the young were then recorded.   In order to have enough nymphs for a test, it was necessary to use nymphs which hatched at slightly different times.   Because of this variation in time of hatching, the first recorded weighings are for approximately one week old insects.

FIGURE 3.   Normal egg capsules on the left; deformed egg capsules on the right.

The remainder of the second generation rearing procedures were the same as those used for the first generation studies.   However, fresh diets, identical to those employed for the first generation were prepared for the second generation work.

RESULTS AND DISCUSSION OF SECOND GENERATION STUDIES

The results of the second generation experiments in average weight in milligrams per cockroach per week are given in table 4.   These data are presented graphically for the second week, fourth week, and eighth week in figure 4.   They indicate that inhibition possibly began between the second and fourth weeks of rearing. In the eighth week, the second generation cockroaches which were reared on the check diet reached the adult stage.   Here, it appears that second generation cockroaches whose parents received 50 or more ppm. of penicillin (diets 5 to 8) were inhibited in growth.

An analysis of variance of the second generation data indicated that the growth rates were not the same for the various diets (table 5).   Therefore, a test for a significant difference between the check mean and the means of the other individual treatments was performed by the method of Least Significant Difference.   When no difference between the check mean and the treatment mean

was found, there was considered to be no inhibition of growth. When a difference between these means occurred, growth was considered to be inhibited.

From this, it can be seen that although inhibition of growth in the first generation was not evident until 780 ppm. of penicillin were present in the diet, the offspring of cockroaches which received as little as 50 ppm. exhibited reduced growth rates. This inhibition appeared whether the young were reared on the

TABLE 4

Weights of second generation roaches on test diets

Diet Number	Initial	1	2	3	4	5	6	7	8
1 (check)	——	2.43*	3.63	6.80	10.50	16.23	24.70	33.76	44.86
2	——	2.20	3.46	7.96	12.06	17.13	24.12	33.03	42.75
2'	——	2.40	3.32	8.00	10.37	15.38	23.44	32.25	40.90
3	——	2.58	3.55	6.41	9.86	14.06	22.30	29.38	37.74
3'	——	2.61	3.46	6.45	9.77	16.32	21.61	30.55	35.62
4	——	2.60	3.08	4.30	11.08	16.11	20.69	33.44	47.80
4'	——	2.03	2.68	7.42	10.36	15.47	23.31	20.57	41.50
5	——	1.86	2.70	4.57	7.63	9.14	13.14	17.71	21.96
5'	——	2.10	3.06	4.56	7.84	8.08	12.20	14.79	21.20
6	1.14	2.48	4.19	6.21	8.04	12.28	17.08	17.31	25.86
6'	——	1.87	2.98	4.66	7.04	7.93	11.85	12.73	17.10
7	——	2.02	3.26	4.42	6.50	7.92	10.39	11.92	14.89
7'	——	1.69	2.56	6.35	7.27	9.23	10.31	10.81	15.73
8	——	2.00	2.81	4.01	5.03	7.05	8.27	10.59	13.07
8'	——	2.00	3.54	5.00	6.34	8.46	10.00	12.46	13.50

*The two replicates of approximately 30 insects each agreed well as to toal weight, and only the average of the two is recorded. Complete data are on file in the editor's office or may be obtained from the author upon request.

TABLE 4 continued

Weights of second generation roaches on test diets

Diet Number	9	10	11	12	13	14	15
1 (check)	——§	——	——	——	——	——	——
2	——	——	——	——	——	——	——
2'	——	——	——	——	——	——	——
3	46.01	——	——	——	——	——	——
3'	50.65	——	——	——	——	——	——
4	——	——	——	——	——	——	——
4'	——	——	——	——	——	——	——
5	31.50	37.27	44.15	——	——	——	——
5'	29.88	36.86	44.53	——	——	——	——
6	34.55	46.88	——	——	——	——	——
6'	19.12	24.08	30.26	38.24	44.38	——	——
7	18.08	22.22	26.94	29.80	37.48	44.60	——
7'	18.99	26.08	32.61	38.57	44.04	——	——
8	10.02	18.74	24.41	28.78	34.11	33.27	44.07
8'	20.34	21.32	27.40	32.55	36.26	43.40	44.67

'Indicates use of parental diet. The check diet was used for the others.
§No records because the cockroaches had reached the adult stage.

control diet or on the parental diet. Therefore, it is concluded that in the first generation reared on diets containing 50 to 400 ppm. of penicillin, some irreparable damage occurred which was not evident until the second generation.

Figure 5 represents, graphically, the time in weeks in which the cockroaches reached the adult stage when reared on the various diets. Increase in time occurred chiefly if the parents of the young received 50 or more ppm. of penicillin, regardless of whether the young were reared on the check diet or on the parental diet.

In general, second generation cockroaches exhibited higher mortality than the first generation cockroaches, even if their parents received as little as 100 to 200 ppm. of penicillin.
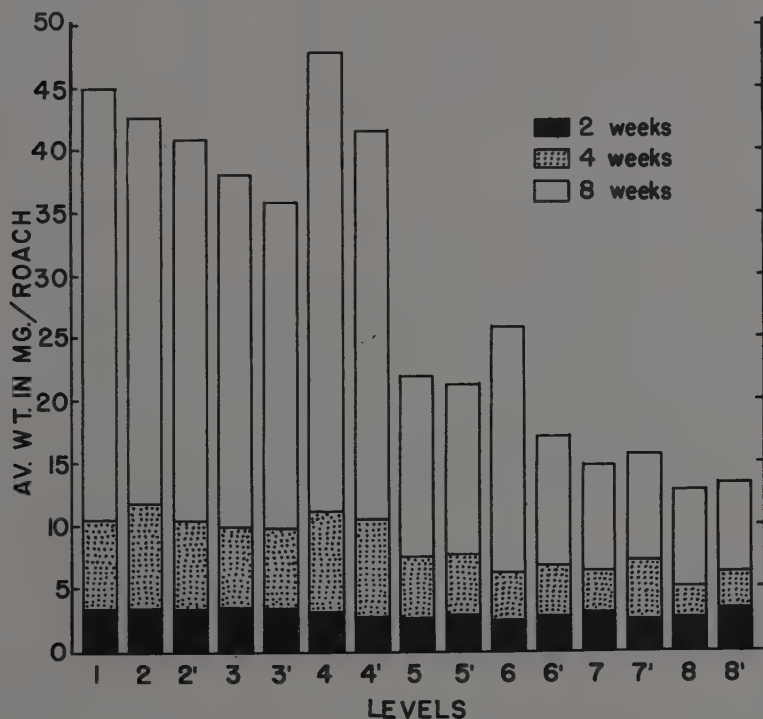
FIGURE 4. Growth of the second generation cockroaches at two, four, and eight weeks, when reared on the control and parental diets. (Primed numbers represent cockroaches reared on the diets of their respective parents; unprimed numbers represent cockroaches reared on the check diet.)

Second generation cockroaches, reared on either control or parental diets, appeared to reproduce normally if their parents received less than 50 ppm. of penicillin. However, third generation young produced by roaches whose parents received 50 to 100 ppm. of penicillin, hatched later than normal. Also, fewer nymphs per capsule were produced.

Cockroaches whose parents received 100 or more ppm. of antibiotic produced fewer egg capsules and these were often deformed. Again, this resulted regardless

of whether the second generation young were reared on the control or on the parental diets.

Experiments in rearing the young from adults receiving more than 400 ppm. of penicillin were rather limited and therefore inconclusive. In general, only enough insects were available to set up one replication. However, sometimes, not even the necessary 30 were available. On the average, these cockroaches reached the adult stage in about 13 to 16 weeks, regardless of whether they were reared on the control or parental diet. This was the case with 50 young from adults reared on diet 10 (1,560 ppm. of penicillin). The 50 young used for the test, however, were the total from fifteen egg capsules. Since a female cockroach normally produces 30 to 45 young per egg capsule, this sample was not considered adequate to reach any conclusions concerning the young which were produced.

Although fewer young were produced by adults receiving high concentrations of penicillin, those which did appear did not manifest all the characteristics shown by the aposymbiotic cockroaches which resulted from the work of Brooks and Richards (1955) with aureomycin at a level of 1000 ppm. They reported these nymphs possessed the following characteristics: 1) the nymphs were slightly smaller than normal and light gray in color rather than dark blackish brown; 2)

TABLE 5

Analysis of variance of the growth rates with second generation diets

Source	SS	DF	MS	F	F–5%	F–1%
Treatments	.4151	14	.02965	6.3545*	2.43	3.56
Error	.0700	15	.0046			
Total	.4851	29				

*Significant at 1% level.

Growth time equals the entire growth period. Test based on two replications of approximately 30 insects each, per treatment.

the embryonic cuticle, which is normally shed at the time of hatching, was not completely cast, but remained attached to the anal cerci; 3) the nymphs were weak and feeble; 4) some nymphs died immediately, while others lay on their backs for several days waving their antennae; and 5) the nymphs were almost completely unable to grow on the stock dog food diet. The controls molted approximately every 10 days on the dog food diet, and reached the adult stage at about 60 days. The young aposymbiotic nymphs had not molted once by the end of 30 days.

In this study, the offspring from adults receiving as much as 50,000 ppm. of penicillin did not show all of the above listed characteristics. The color appeared normal in about half of the insects, and the embryonic cuticles were completely detached. In addition, those that lived were able to reach the adult molt in 13 to 14 weeks on the normal dog food diet. This was not even twice the normal growth period. Antibiotics differ considerably in structure and mode of action. Therefore, it is quite likely that with dietary penicillin, the bacteroids were not eliminated or only partially so, and that the effects of the penicillin were directly on the cockroaches.

However, in all respects, the second generation cockroaches were much more adversely affected than the first.

SUMMARY

1. Some effects of the oral administration of penicillin on the German cockroach were studied. The antibiotic was added to a dog food diet at fifteen different

levels of concentration ranging from six to 100,000 ppm.   Starting with six ppm., each succeeding dietary level increased geometrically by a factor of two.   The insects were fed the various diets all their lives and through two successive generations.

2.   The effects studied were: the growth rate; time to the adult stage; mortality; reproductive capacity; and these same effects in the second generation.

3.   Test growth rates in the first generation appeared to be equivalent to the check if the particular diet did not contain more than 400 ppm. of penicillin. At 780 ppm. or more, inhibition of growth was significant and became increasingly more severe up to 100,000 ppm.   In the second generation, the offspring of the cockroaches which received as little as 50 ppm. exhibited reduced growth rates, regardless of whether they were reared on the control or parental diet.

4.   First generation cockroaches receiving diets containing less than 780 ppm. of penicillin reached the adult stage in approximately the same length of time. In levels containing 780 or more ppm., however, there was an inverse relationship between time to adult stage and growth rate.   Offspring from first generation
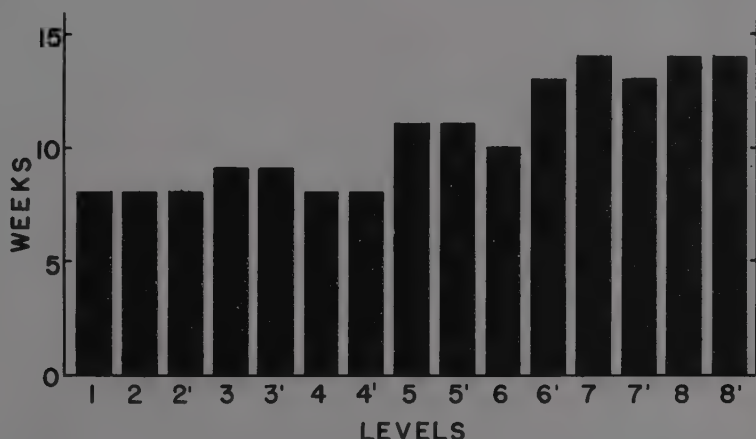
FIGURE 5.   Time in which the second generation cockroaches reached the adult stage, when reared on diets containing different concentrations of penicillin.   (Primed numbers represent cockroaches reared on the diets of their respective parents; unprimed numbers represent cockroaches reared on the check diet.)

adults receiving 50 or more ppm. of penicillin required a longer time to reach the adult stage than did the checks.

5.   The first generation test cockroaches exhibited no appreciable mortality over the checks, even at the highest dietary levels of penicillin concentration. Second generation cockroaches exhibited higher mortality than the checks if their parents received as little as 100 to 200 ppm. of penicillin.

6.   Reproductive capacity was apparently reduced in all dietary levels containing 200 or more ppm. of penicillin.   No eggs were formed by the cockroaches receiving the diet containing 100,000 ppm. of penicillin.   Offspring of adults receiving diets containing 50 or more ppm. of penicillin exhibited reduced reproductive capacity.

7.   In all respects, the second generation cockroaches were much more adversely affected than the first.

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A NEW SUBSPECIES OF *CHRYSOBOTHRIS BIRAMOSA* (FISHER)

(COLEOPTERA: BUPRESTIDAE)

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Chrysobothris biramosa calida n. subsp.

This form differs from typical *C. biramosa* (Fisher) by the brilliant green occiput, pronotum and elytra. The three transverse blue bands on each elytron are similar to those of *biramosa biramosa*. Holotype: length 8.4 mm.; width 3.5 mm.

It superficially resembles *C. atrifasciata* Lec. which has a green head and ventral surface; pronotum is wider in proportion to length; sculpture of head, pronotum and elytra is much coarser.

Holotype ♂ collected in Santa Rosa Mountains, Riverside Co., Calif., June 25, 1946 by D. J. and J. N. Knull. Allotype and two paratypes labeled Blythe, Riverside Co., Calif. May 17, 1937, E. D. Algert. Other paratypes Yuma, Yuma Co., Arizona, June 19, 1935, O. Bryant and Ehrenberg, Yuma Co., Arizona, June 26. F. H. Parker, in collection of author.

VARIATION IN *HELIOPSIS HELIANTHOIDES* (L.)
SWEET (COMPOSITAE)[1]

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INTRODUCTION

Heliopsis helianthoides is composed of three subspecies. The distribution of ssp. *helianthoides* is centered in the eastern United States, namely the Appalachian Mountain region where it occurs in wooded, or partially shaded, moist areas. The distribution of ssp. *occidentalis* is centered in the northern Great Plains growing in the dry, open prairie. The third subspecies, ssp. *scabra*, is centered in the Ozark Mountain area and the lower Great Plains region where it grows on dry glades, wooded slopes and valleys. Morphologically these three subspecies are distinct in their own centers of distribution (fig. 1). Subspecies *helianthoides* is charac-
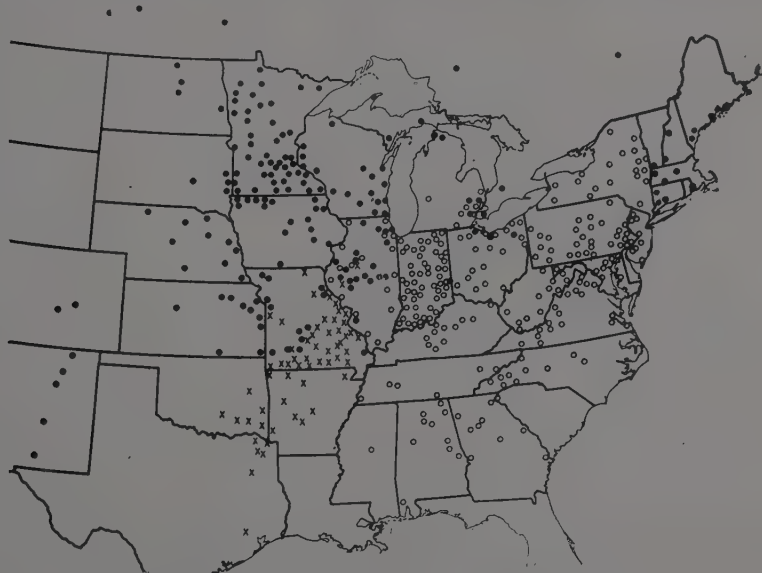
FIGURE 1. Distribution of *Heliopsis helianthoides* in United States and Canada (ssp. *helianthoides*, open circles; ssp. *occidentalis*, solid circles; ssp. *scabra*, X).

terized by glabrous stems and leaves, short peduncles, small heads, and broad ovate-lanceolate leaves with long petioles, whereas ssp. *occidentalis* is characterized by scabrous leaves and upper stems, long peduncles, large heads, and deltoid leaves with short petioles. Subspecies *scabra* is characterized by scabrous leaves and upper stems, long peduncles, heads nearly as large as those of ssp. *occidentalis*, and rather narrow ovate-lanceolate leaves with long petioles.

In a preliminary study of the variation of *Heliopsis helianthoides* (Fisher, 1952), it was shown from a transect study of herbarium material which had been collected within a hundred miles of a line arbitrarily drawn from North Dakota to Virginia, that the species exhibited a very gradual change in its morphological characters from one extreme of the geographical range to the other. Since the preliminary study, a statistical approach to the study of variation of this taxon has been pursued more extensively.

METHODS

Although both living and herbarium material were used in this study, most of the data assembled are from herbarium material borrowed from the major herbaria of the United States. After the range of distribution for *Heliopsis helianthoides* was determined, a map of the area was divided into quadrats of approximately 125 square miles each. Herbarium material was then assembled according to quadrat and measured for leaf blade-petiole angle, petiole length, peduncle length, head width, and pubescence (table 1).

The leaf to be used for measurement was selected from the fourth node below a mature head, since the shape of the leaf was observed to change during the

TABLE 1

Measurements of four characters of Heliopsis helianthoides *from herbarium material assembled into equal-area quadrats.* (*Means, standard deviation and coefficients of variation; angles in degrees, length and width in centimeters.*)

QUA-DRAT	LEAF BASE ANGLE			PETIOLE LENGTH			PEDUNCLE LENGTH			HEAD WIDTH		
	$\overline{X}$	s	v	$\overline{X}$	s	v	$\overline{X}$	s	v	$\overline{X}$	s	v
B–14	97.0	12.1	12.4	.52	.24	4.61	20.18	5.90	2.92	1.82	.3	1.6
C–11	104.2	8.4	8.0	.6	.3	5.7	22.7	3.1	1.3	1.6	.3	1.7
C–12	100.0	9.5	9.5	.4	.3	6.8	19.6	5.4	2.7	1.8	.1	.7
C–13	105.1	7.2	6.8	.7	.3	4.8	18.6	5.4	2.9	1.7	.3	2.2
D–2	109.8	8.3	7.5	1.0	.3	3.2	17.2	5.3	3.0	1.5	.1	1.1
D–7	105.0	2.6	2.4	.7	.4	6.7	17.0	7.3	4.2	1.7	.4	2.8
D–8	107.0	16.5	15.4	1.1	.2	2.5	18.0	8.6	4.7	1.5	.5	3.4
D–11	102.0	8.6	8.4	.8	.2	2.5	17.0	5.8	3.4	1.7	.3	1.7
D–12	103.0	9.2	8.9	.5	.3	6.0	18.5	3.7	2.0	1.7	.5	2.9
E–1	112.0	18.2	16.2	1.6	.7	4.6	16.0	8.4	5.2	1.4	.2	1.4
E–2	111.0	9.0	8.1	2.6	.4	1.6	14.0	3.7	2.6	1.4	.4	3.2
E–3	112.0	13.5	12.0	2.6	1.1	4.2	12.2	4.7	3.8	1.7	.2	1.4
E–9	100.0	7.1	7.1	.8	.5	6.8	16.0	5.1	3.1	1.6	.3	2.0
E–10	111.0	8.1	7.2	1.5	.3	2.0	15.4	5.6	3.6	1.5	.2	1.4
E–11	101.2	3.4	3.3	.8	.4	5.7	17.8	3.7	2.0	1.8	.1	.5
E–12	102.1	8.1	7.9	.6	.2	3.9	16.9	4.2	2.4	1.7	.4	2.5
E–13	95.2	9.2	9.6	.6	.3	5.4	15.5	5.6	3.6	1.4	.3	2.5
F–1	113.0	4.6	4.0	1.7	.5	3.0	15.2	7.9	5.1	1.4	.2	2.0
F–2	118.0	5.8	4.9	2.2	.5	2.5	14.4	5.6	3.8	1.4	.2	1.7
F–3	116.4	13.0	11.1	2.2	.8	3.7	12.5	4.8	3.8	1.2	.4	4.0
F–4	115.0	6.4	5.5	2.0	.8	4.1	14.1	2.6	1.8	1.6	.4	2.5
F–5	115.2	20.6	1.7	2.7	.6	2.4	8.8	1.2	1.4	1.3	.4	3.3
F–6	115.0	9.0	7.8	1.7	.6	3.8	12.8	3.4	2.6	1.3	.2	1.5
F–8	104.7	6.7	6.3	1.1	.6	5.8	17.4	5.1	2.9	1.7	.2	1.4
F–9	107.8	4.3	3.9	1.1	.4	4.1	17.6	3.1	1.7	1.5	.9	5.8
F–10	105.0	9.6	9.1	1.2	.2	2.3	14.5	6.7	4.6	1.4	.1	.7
F–11	106.3	14.6	13.7	.7	.3	4.8	18.5	6.5	3.5	1.9	.2	1.1
F–12	112.2	11.7	10.4	.4	.2	6.2	14.5	7.2	3.8	1.6	.1	.8
F–13	98.7	6.6	6.6	1.1	.1	.8	11.2	3.4	3.0	1.3	.8	6.2
F–14	99.6	6.7	6.7	1.4	.1	.9	7.6	1.7	2.2	1.4	.1	.9
F–15	96.5	2.6	2.6	1.1	.1	.9	14.7	3.0	2.0	1.3	.2	1.8

TABLE 1—(Continued)

QUA-DRAT	LEAF BASE ANGLE			PETIOLE LENGTH			PEDUNCLE LENGTH			HEAD WIDTH		
	X̄	s	v	X̄	s	v	X̄	s	v	X̄	s	v
G–2	118.0	10.0	8.4	1.8	.6	3.3	11.8	4.6	3.9	1.3	.3	2.7
G–3	115.0	9.5	8.2	1.7	.4	2.6	11.3	4.6	4.0	1.3	.2	1.6
G–4	116.1	10.6	9.1	2.2	.2	1.1	13.5	6.4	4.7	1.4	.3	2.1
G–5	122.0	14.7	12.0	2.1	.4	2.0	10.3	4.1	3.9	1.2	.2	1.8
G–6	125.3	6.9	5.5	1.8	.7	4.0	9.9	2.2	2.2	1.2	.1	.8
G–8	114.2	11.1	9.7	1.6	.5	3.5	13.9	8.0	5.7	1.5	.2	1.6
G–9	118.0	10.9	9.2	1.2	.6	5.2	16.7	4.4	2.6	1.6	.4	2.5
G–10	119.3	14.5	12.1	1.3	.3	2.5	14.0	3.3	2.3	1.4	.2	1.6
G–11	108.7	9.3	8.5	.6	.3	5.3	18.0	1.4	.6	1.6	.7	4.2
G–12	103.2	10.6	10.2	.8	.3	4.4	15.6	5.7	3.6	1.6	.5	3.3
G–13	99.0	5.0	5.0	1.2	.5	4.4	10.0	2.0	2.0	1.7	.1	.5
H–2	119.6	12.0	10.0	2.4	.5	2.4	11.2	6.1	5.4	1.2	.2	2.1
H–3	122.5	14.5	11.8	1.9	.5	2.5	13.0	4.2	3.2	1.2	.5	4.1
H–4	116.0	10.0	8.2	2.2	.5	2.5	13.0	3.3	2.5	1.4	.4	2.9
H–6	124.8	13.0	10.4	2.1	.4	2.2	10.9	2.8	2.5	1.2	.3	2.7
H–7	114.6	13.9	12.1	1.9	.5	3.0	9.4	4.1	4.3	1.3	.3	2.6
H–8				1.8	.6	3.8	11.4	3.4	2.9	1.4	.1	1.0
H–9	113.7	16.4	14.4	1.2	.4	3.5	16.1	5.0	3.1	1.6	.2	1.7
H–10	116.8	9.2	7.8	1.7	.5	2.9	11.1	5.9	5.3	1.3	.2	1.5
H–11	112.3	11.2	9.9	.6	.3	5.5	13.5	3.4	2.5	1.6	.5	3.6
H–12	101.1	9.5	9.3	1.1	.5	4.8	15.7	5.0	3.1	1.7	.4	2.4
H–13	107.2	8.9	8.3	1.0	.6	6.3	15.8	7.8	4.9	1.2	.6	5.5
H–14	104.0	9.4	9.0	.9	.4	4.4	14.5	6.9	4.7	1.7	.5	3.1
I–2	127.7	16.1	12.6	2.0	.5	2.7	10.2	4.6	4.5	.9	.1	1.8
I–4	118.3	12.4	10.4	2.4	.7	3.0	12.4	3.8	3.0	1.2	.3	3.1
I–5	123.6	6.7	5.4	3.1	.9	3.0	10.6	2.0	1.8	.9	.1	1.7
I–6	125.0	9.4	7.5	2.3	.7	3.3	9.5	5.0	5.2	1.1	.3	2.8
I–7	117.5	4.4	3.7	2.2	.6	3.0	7.6	2.4	3.1	1.0	.3	3.8
I–8	125.4	13.0	10.3	1.6	.2	1.6	9.8	3.0	3.0	.9	.3	3.0
I–9	122.0	17.5	14.3	1.5	.6	4.2	12.9	4.8	3.7	1.4	.5	4.1
I–10	128.0	9.1	7.1	1.5	.6	4.4	10.0	3.4	3.4	1.2	.2	1.8
I–12	117.5	14.8	12.5	1.5	.7	4.6	13.7	6.3	4.5	1.5	.4	3.0
I–13	119.2	9.4	7.8	1.1	.4	3.6	12.1	6.8	5.6	1.9	.4	2.1
I–17	98.3	8.0	8.1	.6	.2	3.9	22.1	7.6	3.4	1.8	.4	2.6
J–3	128.4	7.6	5.9	2.2	.4	2.0	9.0	4.8	5.3	1.1	.3	2.8
J–4	122.0	5.5	4.5	2.2	.3	1.6	10.8	3.4	3.1	1.1	.3	3.2
J–5	110.5	2.4	2.1	2.9	.8	2.8	10.8	4.1	3.7	1.2	.5	4.4
J–7	122.6	6.6	5.3	2.3	.8	3.8	9.0	3.0	3.3	1.0	.4	4.8
J–9	128.0	10.0	7.8	1.3	.5	3.8	13.5	4.3	3.1	1.2	.4	3.8
J–10	119.8	3.6	3.0	1.4	.5	3.5	15.7	4.2	2.6	1.2	.2	1.8
J–11	120.8	7.6	6.2	1.5	.1	1.1	17.2	5.5	3.1	1.4	.2	1.3
J–12	124.0	5.3	4.2	1.6	.2	1.6	9.6	2.2	2.2	1.6	.4	2.8
J–17	95.0			1.2			25.0			1.6		
K–5	115.5	3.3	2.8	2.6	.9	3.6	12.3	6.2	5.0	1.3	.4	3.0
K–7	126.6	9.7	7.6	2.1	.6	3.0	8.6	3.3	3.8	.9	.1	1.5
K–9	128.0	6.6	5.1	2.2	.6	3.1	8.8	2.6	2.9	.9	.2	2.5
K–11	119.2	9.7	8.1	1.4	.2	1.5	13.3	2.2	1.6	1.2	.4	3.4
K–12	105.0			1.3			8.0			1.2		
K–17	104.8	4.3	4.1	.6	.5	.8	23.5	6.0	2.5	1.8	.5	3.2
L–11	128.6	10.4	8.0	1.0	.4	3.7	15.0	3.8	2.5	1.0	.2	2.0
L–12	127.8	4.3	3.3	1.2	.9	6.7	17.7	4.8	2.7	1.1	.3	3.2
L–13	123.0			1.3			13.0			1.4		
L–17	105.8	6.6	6.2	.8	.1	2.0	20.7	3.2	1.5	1.7	.2	1.1
M–12	118.6	6.6	5.5	1.5	.2	1.7	17.1	6.3	2.3	1.2	.3	3.0
M–18	106.5	7.4	6.9	.7	.5	6.4	20.5	6.3	3.0	1.6	.3	2.3

growing period of the plant.   When the leaf was poorly preserved, it either was
not measured or was first removed and boiled in water until it could be sufficiently
flattened for measurement.   The leaf was then dried again and replaced on the
herbarium sheet.   Only sheets with abundant material were used in this manner.
Type or other authentic specimens were not used for the statistical study.

The leaves of ssp. *helianthoides* tend to be broadest near the middle of the leaf
and taper to the petiole, whereas ssp. *occidentalis* tend to be broader below the
middle and contract sharply into the petiole.   The leaves of ssp. *scabra* are also
ovate but more lanceolate in shape, otherwise appearing at the base about the
same as ssp. *helianthoides*.   Since these extreme leaf shapes exist in this taxon it
was felt that a method was desirable by which the angle formed by the base of
the leaf blade and the petiole could be measured.

The leaf blade-petiole angle was measured by locating a line AB merely by
following the midrib and petiole of the leaf (fig. 2).   The widest point of the leaf
was then determined and chords CD and EF were drawn parallel to AB, or the
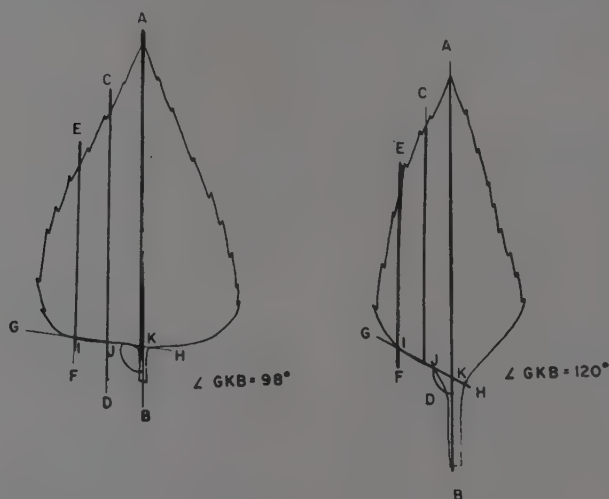
FIGURE 2.   Method for measuring leaf base-petiole angle.   See text.

midrib-petiole, through points one-third and two-thirds of the distance between
the midrib and the widest point on the leaf, respectively.   Points I and J are
located where chords CD and EF transect the base of the leaf margin.   A straight-
edge when placed along points I and J locates the point at which the petiole joins
the blade.   A protractor when placed along the straight-edge offers ready measure-
ment of angle GKB or the leaf base-petiole angle.   In figure 2 it can readily be
seen that angle GKB would measure nearly 90° in a truncate leaf, and much
greater than 90° in an ovate type with a cuneate base.   With the exception of the
leaf base-petiole angle, this can most easily be accomplished by transposing a
transparent millimeter grid on the leaf and reading to the nearest millimeter.
This is a modification of the method used by Woodson (1947) for determining the
leaf shape in *Asclepias tuberosa*.

The statistical treatments have been limited to calculation of mean, standard
deviation, standard error, and the coefficient of variation.   The statistical values

are not projected onto the data maps.   Instead it seems more desirable to illustrate the variation pattern in these species of *Heliopsis* by a more graphic method (fig. 3 and 4).   The single vertical bar in figure 3 represents the mean value for petiole length.   The angle subtending the vertical bar represents the mean value for leaf blade-petiole angle.   Pubescence was scored on a 0 to 4 scale, the 0 end of the scale representing glabrous plants and the 4 end of the scale representing scabrous plants.   The two remaining characters studied, namely head width and peduncle length, are represented in figure 4. Head width values are represented by a solid circle while mean peduncle values are represented by a subtending vertical bar.

<div align="center">RESULTS</div>

<div align="center">*Variation in Petiole Length and Leaf Blade-Petiole Angle*</div>

Upon examination of figure 3 it is evident that there are no well defined limits between the subspecies in respect to petiole length and leaf blade-petiole angle. Instead, there is an even gradient or cline extending not only from the eastern to the western portions of the species range, but also extending north and south.
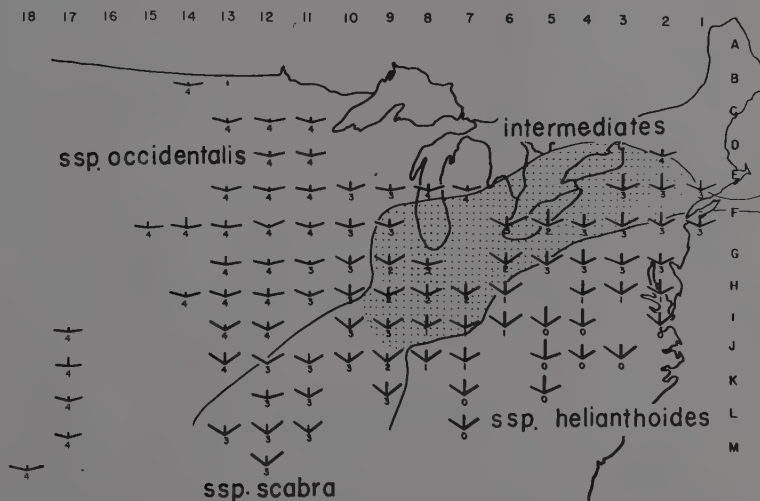
FIGURE 3. Graphic representation of quadrat means for petiole length (vertical bar), leaf blade-petiole angle (subtending angle), and index values for pubescence. Stippled area indicates zone of intermediates between subspecies.

In respect to petiole length, the range of "pure" ssp. *helianthoides* is represented by the 2.0 to 3.1 cm. zone in the eastern area, while the range of "pure" ssp. *occidentalis* is represented by the 0.4 to 0.9 cm. zone in the northwestern portion of the species range.   The 1.0 to 1.9 cm. zone (stippled area) represents intermediates between these taxa.   *Heliopsis helianthoides* ssp. *scabra*, which is centered in the Ozark Mountain area, exhibits the same range of measurements as the intermediates separating ssp. *helianthoides* and ssp. *occidentalis*.   There is a rather sharp disjunction of measurements in regard to petiole length separating ssp. *occidentalis* and ssp. *scabra*.   There is no disjunction of this character between ssp. *scabra* and the intermediate zone of plants.

Variation in leaf base-petiole angle (fig. 3) again indicates a very gradual variation pattern oriented east and west as well as north and south. The range for "pure" ssp. *helianthoides* was determined to be between 120° and 128°, while ssp. *occidentalis* was found to possess leaf blade-petiole angles ranging from 95° to 109°. The distributional range limits of ssp. *scabra* of the Ozark region are ill-defined in regard to this character. The statistical values of this subspecies are within the range of measurements of the plants of the intermediate zone between ssp. *occidentalis* and ssp. *helianthoides*.

There is, on the average, a 10 degree differential in measurements for the leaf blade-petiole angles separating ssp. *occidentalis* and ssp. *scabra*. This indicates a rather definite limit of distribution for these two subspecies in regard to this character. On the other hand, ssp. *scabra* cannot be separated from ssp. *helianthoides* on this basis.
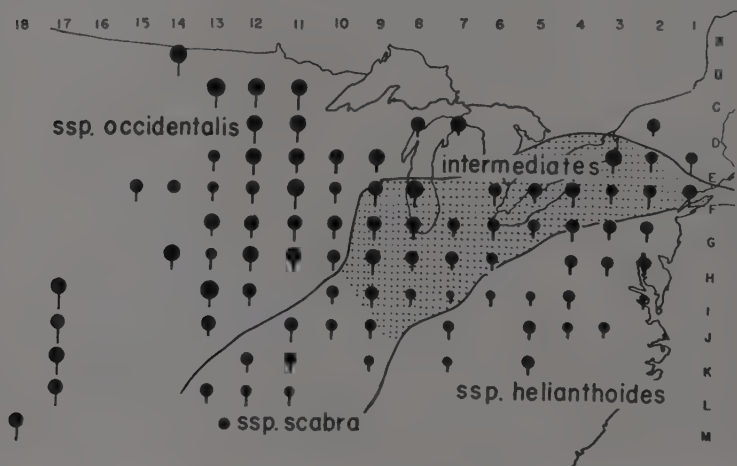
FIGURE 4. Graphic representation of quadrat means for head width (solid circles) and peduncle length (subtending vertical bar). Stippled area indicates zone of intermediates between subspecies.

Variation in Peduncle Length and Head Width

Peduncle length and head width values are represented in figure 4. These two characters have essentially the same pattern of variation as was found in the leaf blade-petiole angle and petiole length. Subspecies *helianthoides* was found to possess peduncle length values ranging from 7.0 to 12.0 cm., while ssp. *occidentalis* varies from 14.7 to 23.7 cm. Between these two taxa (stippled zone) there is a zone of plants with intermediate values which nearly parallels the intermediate zone of the other characters analyzed.

In respect to peduncle length values, ssp. *scabra* is again intermediate between ssp. *occidentalis* and ssp. *helianthoides*. In general there is no discontinuity of measurements for peduncle length separating ssp. *scabra* and ssp. *helianthoides*. On the other hand, there is discontinuity of measurements for peduncle length separating ssp. *occidentalis* and ssp. *helianthoides* along the northwestern limits of the intermediate zone.

The overall statistics for peduncle length show definite clines or gradients oriented between ssp. *helianthoides* and ssp. *occidentalis*, and between ssp. *occidentalis* and ssp. *scabra*, but not between ssp. *helianthoides* and ssp. *scabra*.

The projection of data for head width indicates the same type of character gradient as for the previous characters analyzed. The range of head width values for "pure" ssp. *helianthoides* is 0.9 to 1.2 cm., while the 1.6 to 1.9 cm. zone represents "pure" ssp. *occidentalis* (fig. 4). There is no discontinuity of measurements for head width values separating ssp. *occidentalis* and ssp. *scabra*. There is a gradual cline from the Ozark Mountain area to the northern plains area. There is also a very gradual cline from the northern plains area into the intermediate zone of the midwest. There exists a zone of head width measurements projecting sharply southward along the Appalachian Mountains. It is difficult to account for this projection of head width values. Although environmental influence is not entirely discounted, it is difficult to see how it is a valid reason since the other characters analyzed did not show a similar pattern. It is not implied that the same environmental influence would necessarily have the same influence on all characters.

In general there is no discontinuity in measurements for head width values separating the taxa of of *Heliopsis helianthoides*.

Variation of Pubescence

Prior to this study the taxa of *Heliopsis* found in the United States were separated on the basis of pubescence. Pubescence values exhibit a very gradual gradient from completely glabrous plants of the southeastern portion of the species range to scabrous plants of the upper Great Plains. Plants with a pubescence value of 4 have a range closely corresponding to the range of "pure" ssp. *occidentalis*, while plants with a pubescence value of 0 to 2 have a range closely corresponding to the range of "pure" ssp. *helianthoides*. Between the ranges of these two taxa is found a zone of quadrats with intermediate pubescence values of 2 and 3 (fig. 3).

Subspecies *scabra* is characterized by a pubescent value of 3, nearly agreeing with ssp. *occidentalis* in this regard. The intermediate zone between ssp. *occidentalis* and ssp. *helianthoides*, on the other hand, is characterized by pubescence values ranging from 1 to 3. There is discontinuity in pubescence values separating ssp. *helianthoides* and ssp. *scabra*.

DISCUSSION AND CONCLUSIONS

Although these subspecies are morphologically and ecologically distinct within their respective centers of distribution, they are highly interfertile (Fisher, 1957). The artificial F_1 hybrids exhibit only a slight decrease in fertility. From an examination of present data it is evident that typical ssp. *helianthoides* and ssp. *occidentalis* are connected by a broad band of intermediates, covering an area of several hundred miles. The transition between these areas is very gradual for most characters analyzed. There is no disjunction either in distribution or in characters, except in northeastern United States. Here very little, if any, intergradation can be detected. In Michigan where the two taxa overlap, it is difficult to assign a subspecific epithet to any given plant. When a plant from Virginia is crossed with a plant from Minnesota, the hybrid resembles a plant from Indiana or Illinois. The intermediate zone between these two subspecies extends from northwestern Illinois and southwestern Wisconsin into Central Ohio.

Subspecies *occidentalis* intergrades to a much lesser extent with ssp. *scabra*, but hybridization is apparent in northeastern Kansas, northwest and northeast Missouri where the ranges of the two taxa overlap. The artificial cross between these taxa is easily made and the hybrids are similar to many herbarium specimens collected by Rev. B. F. Bush who collected extensively in Missouri. Many of his

specimens were collected in the same locality and distributed to the various herbaria of this country. If these specimens can be considered a population sample, and essentially they are, even though they were collected on different occasions, a typical hybrid swarm can be reconstructed. Typical specimens of both parents as well as many intermediates can easily be detected. From herbarium specimens and living material observed and collected by the author, it appears that back crossing and subsequent introgression of characters occurs at about the same rate in either direction. The factor most responsible for keeping these two taxa apart is probably ecological, since the habitat preference of the two taxa is quite different. Subspecies *scabra* is found most commonly on the relatively dry ridges and slopes in the Ozark mountain region while ssp. *occidentalis* occurs chiefly in the prairie regions of the Great Plains. Partly discontinuous character clines would be expected with more or less distinct habitats. Subspecies *scabra* apparently does not intergrade with ssp. *helianthoides*. This suggests that a barrier, other than a reproductive one, must be present which keeps these two taxa apart.

In an attempt to explain the pattern of variation in *Heliopsis helianthoides* it is necessary to consider three hypotheses. First, mutation, recombination, and natural selection within the taxa must be considered as a possible explanation of the character gradients or clines. Second, extensive hybridization with repeated backcrossing where the ranges of the taxa overlap seems probable. Third, a combination of these two hypotheses seems likely.

Character clines are probably very common among plant species, but the usual methods of taxonomy, which deal with combinations of characters and aim at detecting discontinuities, are likely to permit them to go undetected. Among the best examples of clines is the one reported by Fassett (1942) in *Diervilla lonicera*. He found that a cline of pubescence ranged from 80 percent frequency at Espanola, Ontario, to 0 percent frequency at Callander, slightly more than 100 miles east.

Gregor (1939) recognized two types of clines in *Plantago maritima*, the topocline and the ecocline. The topocline is similar to the geographic cline which expresses quantitative characters such as the length and width index values of bracts and sepals. Ecoclines are clines related to ecological gradients within a restricted area.

Woodson (1947), in his study of variation in *Asclepias tuberosa*, has shown three definite centers of distribution, namely the Ozark, Appalachian and Orange Island regions. He concludes that reciprocal introgression has occurred from initial hybridization through backcrossing, producing a more or less perfect gradation of the genotype from the Appalachian region in the eastern portion of the species range to the Ozark region in the midwest.

Clausen (1951) has found that character clines do not actually exist in *Layia platyglossa* from studies conducted on races grown in a uniform research garden where the influence of differences in the environment in producing modifications was reduced to a miimum. He states that clines are not commensurable with natural entities, and are oversimplified abstractions dealing with the variation of individual characters. *Layia platyglossa* then, according to Clausen, shows characteristic trends in variability and these trends indicate evolutionary discontinuities.

Assuming that *Heliopsis helianthoides* occupied at one time the eastern part of the United States, namely the Appalachian region where the climatic and associated environmental factors are relatively constant, and migrated toward the Great Plains where the transition in such environmental influences is gradual, then clinal or ecotypic variation might be prevalent. This could be due to gene mutation, gene recombination, and natural selection occuring as the species migrated from one ecological area to another.

If natural selection and not hybridization is the primary cause of variation in *Heliopsis helianthoides*, and it is not implied that natural selection is divorced from

gene mutation and recombination, but rather are complimentary forces, then the gene complexes are a reflection of the environmental complexes. Mutant genes might drift through the populations and might acquire selective value, when the species migrated into new or slightly different environments. As Stebbins (1950) has pointed out, the direction of evolution is determined largely by selection acting on the gene fund already present in the population, the component genes of which represent mutations that have occurred many years before.

Natural selection is an important factor in perpetuating an accumulation of small genetic changes. Populations are, after all, mixtures of several biotypes which differ in fitness for different environments. Thus, when seeds of a plant are scattered to a slightly new or different environment, the species, if its genotype is already modified through gene mutation and recombination, may persist and migrate from one ecological area to another.

The second explanation of these clines is hybridization of individuals of either subspecies where their ranges of distribution overlap. It is not enough merely to account for this phenomenon by hybridization alone without including introgression, *i.e.*, gene flow between interfertile taxa through their hybrids. This has been termed introgressive hybridization by Anderson and Hubricht (1938) and is commonly referred to as introgression. The theory is based on the assumption that partial geographic isolation and morphological diversification precedes reproductive diversification.

The centers of distribution of the three subspecies of *Heliopsis helianthoides* are easily detected as the upper Great Plains, the Ozark, and the Appalachian regions. During the Cretaceous Era, North America was dissected by inland seas of water which extended up the present Mississippi valley as far as southern Illinois. This embayment separated the ancient Appalachian and Ozarkian plateaus. The withdrawal of the Cretáceous seas brought about the reunion of the Ozark and Appalachian plateaus, but by the Pleistocene, continental ice sheets extended as far south as the Missouri and Ohio River valleys with the exception of the driftless area of Wisconsin, northeast Iowa and northwest Illinois (Finch and Trewartha, 1949). Neither did the glaciated area extend farther west than southwest North Dakota and central South Dakota and east central Nebraska.

The above described disturbances could easily have brought about separation of the putative ranges of ssp. *occidentalis*, ssp. *scabra*, and ssp. *helianthoides*. Undoubtedly at the close of the Pleistocene the retreat of the ice created new habitats into which many species of plants dispersed. With colonization of these new habitats these subspecies of *Heliopsis* could have undergone wholesale hybridization and backcrossing. Following this initial phase of hybridization to the present day, introgression has produced a zone hundreds of miles wide, represented by plants intermediate in phenotypic characters between relatively uniform phenotypes at either geographic extreme of the species range.

At the onset of hybridization between two taxa, standard deviations of populations within the zone of hybridization would oridinarily be expected to show higher values than later. In *Heliopsis* this is not seen; instead, quadrats with high standard deviation values seem not to follow any set pattern. For this reason quadrats with high standard deviation values are accounted for by excessive variation of the environmental factors in the area in which the taxon grows. Furthermore, the quadrats in the intermediate zone, assuming introgression pressure is equal between the subspecies, might be expected to yield higher mean values due to heterosis (except in angle measurements). This is apparently true in *Asclepias tuberosa*, and Woodson (1947) has termed it the "crest of variability."

If the process of hybridization and extensive backcrossing has been going on over a considerable period of time to the extent that a genetic "leveling" effect has been reached, the plants of the intermediate zone would not necessarily express high standard deviation values. It has been repeatedly observed during the

course of this investigation that the variation is not between individuals of the population, but between populations.

It is not implied that during the period of putative hybridization of the two taxa, gene mutation, recombination, and the influence of the various environmental factors would not be present and operative. This does, however, suggest a third hypothesis, that is, a combination of the above two hypotheses as a possible explanation of the variation found in this species.

It is very difficult to assign definitely one or the other of the above hypotheses to the variation pattern in *Heliopsis helianthoides*. Natural selection, although admittedly very important in the evolution of any population or system of populations, cannot completely account for this type of variation from the evidence presented. There is an overall gradual intergradation of characters between ssp. *helianthoides* and ssp. *occidentalis*; but in certain portions of the range, namely Michigan, New York and Vermont, the gradient changes abruptly in respect to most characters. Also there is an abrupt change in some characters analyzed and not in others in portions of the range. Precipitous changes in character gradients when not accompanied by corresponding changes in the environment is evidence against natural selection and favors the theory of hybridization as the primary cause of the variation pattern in *Heliopsis helianthoides*. Theoretically, extensive hybridization and backcrossing between the two taxa over a considerable length of time could produce a broad zone of intermediates which exists between ssp. *helianthoides* and ssp. *occidentalis*. Furthermore, the subspecific taxa are relatively homogenous within their respective centers of distribution. The greatest amount of variation is where the subspecies ranges overlap; therefore, the more logical of the three explanations for the variation pattern is hybridization between the two subspecies.

SUMMARY

Heliopsis helianthoides (L.) Sweet of the United States and Canada has been studied over its entire range of distribution. This species of *Heliopsis* is found to consist of three morphologically distinct taxa, namely ssp. *helianthoides* of the eastern United States, ssp. *scabra* of the Ozark region, and a newly described taxon, ssp. *occidentalis* of the upper Great Plains region. Gradual intergradation of characters was found to exist between ssp. *occidentalis* and ssp. *helianthoides*, and to a lesser extent between ssp. *occidentalis* and ssp. *scabra*. Very little, if any, intergradation exists between ssp. *scabra* and ssp. *helianthoides*.

Three hypotheses have been considered in an attempt to explain the pattern of variation found to exist in this species of *Heliopsis*. First, mutation, recombination, and natural selection within the taxa must be considered as a possible explanation of the character gradients or clines. Second, extensive hybridization with repeated backcrossing where the ranges of the taxa overlap seems probable. Third, a combination of these two hypotheses also seems likely.

ACKNOWLEDGMENTS

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STUDIES ON THE ACOUSTICAL BEHAVIOR OF
SEVENTEEN–YEAR CICADAS

(HOMOPTERA: CICADIDAE: *MAGICICADA*)

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INTRODUCTION

In 1956 the writers studied Brood XIII of the seventeen-year cicadas in
northern Illinois and firmly established the existence of two distinct species (Moore
and Alexander, in press). This was not a new suggestion, but its general lack of
acceptance, even among taxonomists, indicated the need for a summarization of
the evidence. The most drastic differences between the two closely related and
highly sympatric species were found in their songs and singing behavior, and
evidence was presented to demonstrate that the song differences were behaviorally
significant. The suggestion was made that the songs act as congregating mechan-
isms for the adult males and females of each species and concomitantly reduce the
number of interspecific encounters between sexually responsive males and females.
No experimental data were available. Accordingly, in late May of 1957, when it
became apparent that the same two species of *Magicicada* that appeared in Brood
XIII in northern Illinois were appearing in Brood XIV in southern Ohio, field
tests were planned to determine more specifically the role of song in the lives of
these insects. This paper reports the results of those tests.

The Songs of M. septendecim *(Linnaeus) and* M. cassinii *(Fisher) Brood XIV*

Tape recordings and analyses of the songs of Brood XIV cicadas have revealed
little or no variation from the responses of Brood XIII cicadas portrayed in figures
1 to 5, and described in detail by Moore and Alexander (in press). Consequently,
only brief descriptions will be given here to facilitate understanding of the experi-
mental procedure employed and interpretation of the additional information
acquired during the present study.

The congregational song (fig. 1 and 2).—This is the only song produced in

chorus by both species. The individual phrases of the congregational song of *septendecim* (fig. 1) are low-pitched buzzes lasting 2 to 4 seconds and separated by intervals of 0.5 to 2 seconds. Each buzz has a rather narrow band of frequencies between 1 and 2 kilocycles per second and drops noticeably in pitch near its end. The individual phrases of the congregational song of *cassinii* (fig. 2) consist of two parts, a series of 12 to 40 ticks delivered at 16 to 25 per second and followed immediately by a loud, shrill buzz lasting 1 to 2 seconds. This buzz has a wide band of frequencies at about 4 to 6 kilocycles per second, and rises, then falls in pitch. In the song of *septendecim* the sound pulses in the buzz (due to individual vibrations of the tymbals) are delivered at 120 to 160 per second while those in the buzz of *cassinii* are delivered at 180 to 210 per second. These descriptions are based on recordings made at 88 to 90° F.

In both species the rhythm of the congregational song involves short bursts of flight as a result of which the singing individuals continually move from perch to perch. In the songs of individual males one to five song phrases are usually delivered between flight bursts, the number becoming smaller as the species nears the peak of its chorusing activity each day.

The courtship songs (fig. 3 and 4).—In 1956, a single sound for each species was heard during courtship and these were described and considered as analogous. However, during the present study an additional courtship sound has been heard for each species, and these indicate that the two courtship sounds heard in 1956 are not analogous. It is likely that these additional sounds do not reflect any difference between Broods XIII and XIV, but rather are a result of more time spent making detailed observations on Brood XIV in the field. Neither of the new sounds was recorded.

Next to the congregational songs of the two species, the most frequently heard sound in both broods was a prolonged slow ticking (3.6 to 6.7 per second) by *cassinii* males (fig. 4). The only other song noticed in Brood XIII was a rarely heard series of short buzzes by *septendecim* males produced at rates of 3.4 to 4.8 per second (fig. 3). Since these two sounds seemed to be analogous courtship songs, it was considered puzzling, both in 1956 and 1957, that the ticking should be heard so much more frequently than the buzzing. This was finally attributed to the different nature of the two sounds and the fact that the buzzing of *septendecim* is less noticeable in a chorus of its congregational song. Mention of this, however, caused two competent field observers to indicate to the writers that they had previously and independently believed the ticking to be the congregational song of a third species. Consequently, special care was taken to locate and observe males producing this sound during the present study. In all ten of such cases noticed in the field, the singing individual was a *cassinii* male courting a female or scuffling with another male. Both of the sounds heard in 1956 were also noticed to be produced in cages containing only adult males. This could possibly indicate a function other than courtship, but it should be noted that it is not unusual for a male insect to court other males. In the laboratory, five different males were heard to produce the ticking sound on one occasion and later the normal *cassinii* congregational song. These observations all appear to discount the suggestion of a third species, at least in broods XIII and XIV.

In 1957, two sounds were heard in addition to those heard in 1956. The first of these was a prolonged series of short buzzes (3 to 5 per second), apparently produced by *cassinii* males. No male was observed producing this sound, but to the ear it sounded exactly analogous in rhythm to the courtship sound already noticed for *septendecim* (fig. 3). The second new sound was a rapid production of shortened phrases resembling those in the congregational song of *septendecim*, but delivered at a rate of about one per second, with practically no intervening intervals. At first this sound was believed to be produced by an abnormal *septendecim* male since some noticeably deformed individuals had been heard producing

peculiar songs.   However, after hearing this sound several times, it was realized that immediately following a series of 10 to 20 of the phrases, the short buzzes characteristic of courting males of *septendecim* were always produced.   Two individuals producing the new sound were located, and in both cases the male was approaching a female two or three inches away.   In both cases, as the male neared the female he extended his right foreleg and vibrated it rapidly.   Then he began producing the short bursts already described for courtship and sidled close to the female.   In one case the female prevented the male from mounting by extending her wing on the side from which he approached, and in the other case the female walked away and was pursued by the male until he accidentally dropped to the ground.

After these observations, we listened carefully and noticed that in the two cases heard thereafter, the intermittent buzzing of *cassinii* was produced im-
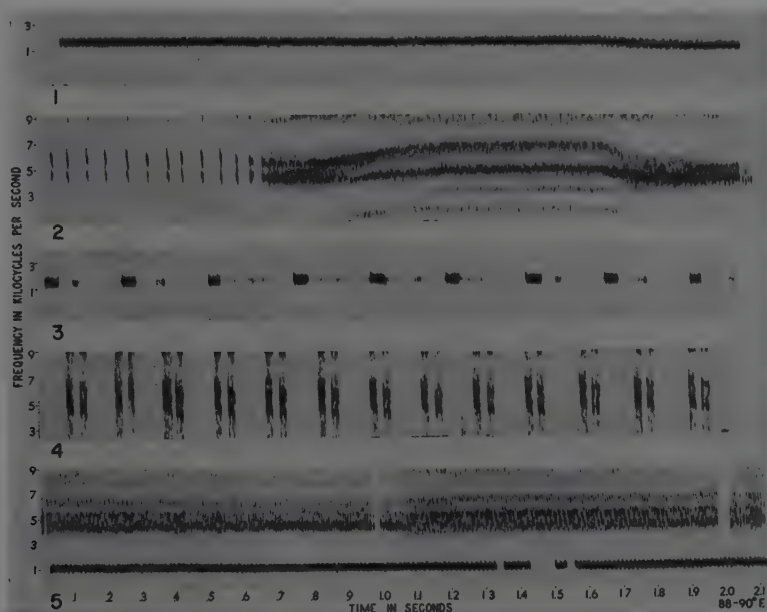
Audiospectrographs of the different sounds of *M. septendecim* and *M. cassinii* (relative intensities shown by darkness of the mark).

    1. A single phrase from the congregational song of *M. septendecim*.
    2. A single phrase from the congregational song of *M. cassinii*.
    3. Several phrases from the song produced in advanced courtship by *M. septendecim* (faint marks are sounds of other individuals).
    4. Several phrases from the song produced in preliminary courtship by *M. cassinii*.
    5. Protest squawking of *M. septendecim* (lower) and *M. cassinii* (upper).

mediately following a series of slowly delivered ticks.   This suggests that in both species there sometimes may be two sounds connected with courtship, and that the ticking of *cassinii* and rapid calling of *septendecim* are analogous to each other and are produced during a later stage of courtship.   This suggestion fits well with the relative frequency with which each of the sounds was heard, as well as with the situations in which they were observed and with their structural relationships.

The series of rapidly delivered calls of *septendecim* is probably obscured most of the time because of its close resemblance to the congregational song.

The significance of the courtship sounds is unknown, but at least four possible functions can be suggested: (1) they may attract responsive females to individual males across short distances; (2) they may be a necessary prerequisite to successful copulation after the male and female have come into close proximity; (3) they may shorten the time between an initial encounter between male and female and subsequent copulation; and (4) a male capable of producing these sounds may successfully copulate with a female simultaneously or just previously courted by males unable to produce these sounds. The courtship sound is only produced when the male and female are in close proximity. The infrequence with which the sounds are heard suggests that they are not produced prior to every instance of copulation. These points seem to suggest the third and fourth possibilities as most likely of those mentioned.

The protest squawks (*fig. 5*). —In both species the males vibrate their tymbals when captured, held, disturbed into flight, or otherwise irritated. These sounds are more or less arhythmical, but because of their frequencies and the rate of vibration of the tymbals they are just as distinctive as the other sounds produced by the two species.

The Chorusing Behavior of Seventeen-Year Cicadas

The congregational song is the only sound produced in chorus by species of *Magicicada*, and the remainder of the paper deals only with these particular sounds.
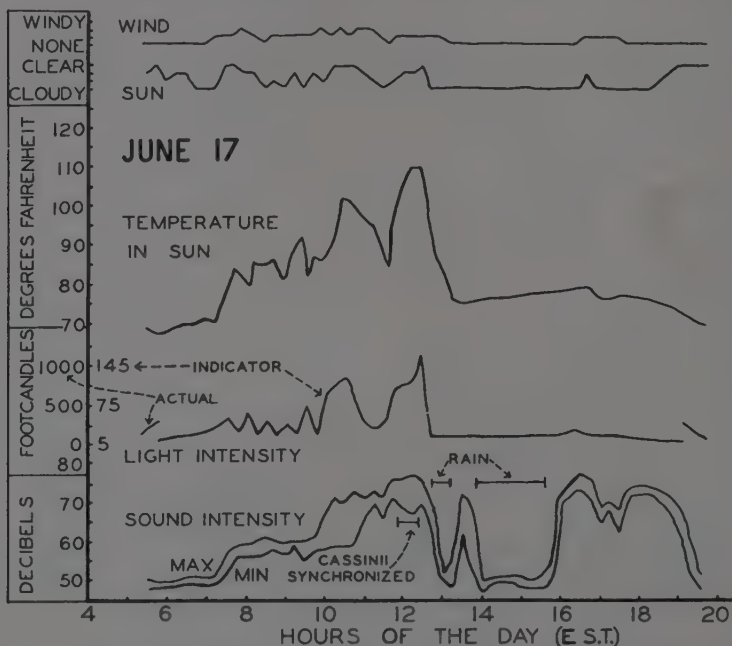
Climatic factors.—Figures 6 and 7 illustrate fluctuations in the chorusing activity of *septendecim* and *cassinii* and in concomitant climatic conditions on a clear, windless day and a cloudy, rainy day, respectively. The observations were made with the equipment set up in the middle of a clearing about 20 feet in diameter in a pasture overgrown with small trees. Temperature was read from a mercury thermometer placed horizontally in the sun (between about 6:45 A. M. and 5:30 P. M.) about six inches above the ground. Light intensity was determined with a Weston Illumination Meter, Model 603. Early and late in the day, readings were taken with the sensitive element facing directly upward. When this became impossible the element was inverted and propped in a set position facing down into the grass from a height of about four inches (fig. 6 and 7, indicatory). Wind and sun were calculated by arbitrarily setting up the categories given in the figure and then subjectively assigning conditions at the time of observation to one of the categories. Sound intensity readings were taken with a General Radio Sound Level Meter, Type 1551-A, using an Amphenol Crystal Microphone, Model 9898. All readings were taken at intervals of 15 minutes or less throughout the day. The maximum and minimum sound intensity readings were taken over a period of about ten seconds.

The nature of the chorusing activity is different for the two species. As mentioned earlier, both species have short bursts of flight incorporated into their singing rhythms as a result of which they may move from a few inches up to several yards from their previous perch. Early in the daily chorusing period, three, four, or more repetitions of the congregational song phrases are produced between flight bursts. As the number of individuals involved in song, the total intensity of the sound, and the uniformity of the sound intensity over the area occupied by the colony increase, fewer song phrases are repeated between flight bursts. In *septendecim* there is no synchronization of song phrases so that the total sound of a colony in full chorus fluctuates little in intensity. In *cassinii* the individuals synchronize their buzzes and when conditions are optimum (about 1 to 4 P. M. on cloudless, windless days and in a strong colony) an incredible degree of synchrony is achieved. Only one buzz is produced by each individual between flight bursts

at this height of activity, and most or all of the ticking is produced during the flight bursts. Almost every singing male in a woods containing tens of thousands of singers achieves synchrony with all the others, and the result gives the impression of a gigantic game of musical chairs. A treeful of these insects singing in synchrony is motionless when observed during the great burst of sound caused by all the males buzzing together, and then becomes a frenzy of activity between buzzes with nearly every individual changing perches. At such times the flutter of wings is so loud between buzzes that it almost obscures the ticking part of the song. The rate and regularity of fluctuations in sound intensity during synchrony by a chorus of *cassinii* are shown in figure 8. This is a line graph drawn from readings of time and sound intensity made simultaneously by two observers. The shape of the curves is nearly symmetrical except for a slight rise (not shown
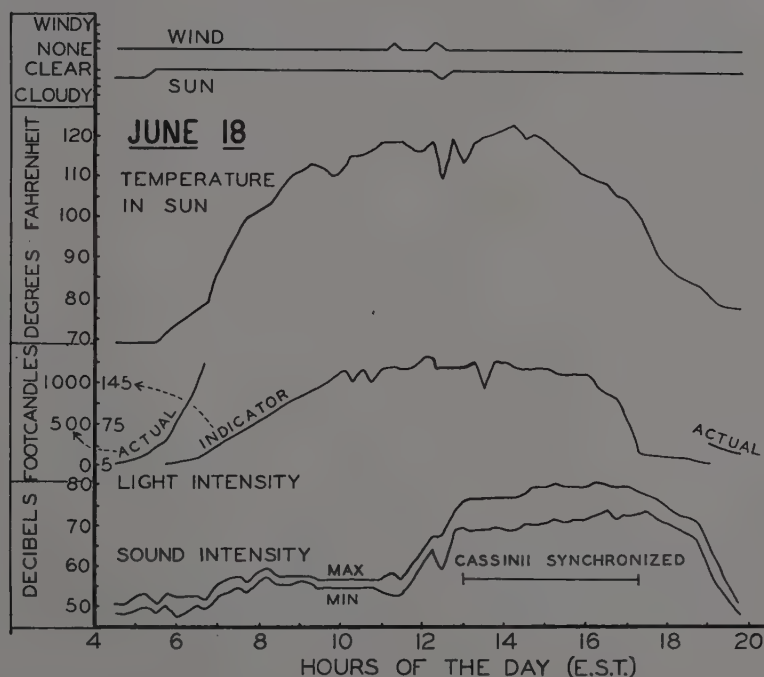
FIGURE 6. Fluctuations in the chorusing activity of *M. septendecim* and *M. cassinii* and in the concomitant climatic conditions on a clear, windless day.

in fig. 8) which occurred about one-half second after the greatest dip and held for a moment before the needle climbed steadily again to a peak. This rise in intensity apparently corresponded with the starting of ticking after the end of the previous buzz. It may be noted that the buzzes of the individual males in a colony are not perfectly synchronized since these last only about two seconds, while 5 to 6 seconds are required for the complete cycle of sound to be produced by the colony. However, the tremendous number of individuals which regularly lump their buzzes together in this short space makes this a high degree of synchrony, perhaps the most remarkable occurring anywhere in the animal kingdom.

The effect of climatic conditions on choruses of *septendecim* and *cassinii* is clearly demonstrated by the various fluctuations in sound intensity in figures 6 and 7. Both species sing only during the day. They chorus more strongly on clear, windless days than on cloudy, rainy, or windy days. They are silent during prolonged rain and during brisk showers, building back up in chorusing activity if the rain stops and the vegetation dries or the sun reappears. Both species appear to be quite sensitive to changes in light intensity, increasing their chorusing activity noticeably at the appearance of the sun in the morning and dropping off in chorusing activity when the sun passes behind a cloud. When the sun reappears from behind a cloud, the intensity of chorusing activity increases, the suddenness and degree of this change corresponding to the suddenness of the reappearance of the sun and the amount of difference in light intensity before and after its reap-

FIGURE 7. Fluctuations in the chorusing activity of *M. septendecim* and *M. cassinii* and in the concomitant climatic conditions on a cloudy, rainy day.

pearance. In the test area, *septendecim* began singing intermittently in early dawn and chorused most strongly on clear, windless days at about 11 A. M., gradually falling off in chorusing activity until only a few individuals were still singing at dusk. *Cassinii* began intermittent singing rather suddenly at sunrise and on clear, windless days generally reached a peak of chorusing activity between 1:00 P. M. and 3:00 P. M., gradually falling off in chorusing activity after this until, like *septendecim*, only a few individuals were singing at dusk. Both species entirely stopped singing in late dusk, and only an occasional squawk could be heard at night. Apparently, little activity other than feeding occurs at night, with copulation and oviposition as well as all normal sound production taking place during

the day.   Pairs frequently remain *in copula* during part of the night after entering into copulation in late afternoon.   Both species appear to oviposit in greatest numbers in early morning and to become involved in copulation in greatest numbers about the time their chorusing activity is beginning to wane.   In one case in the test area a pair of *septendecim* entered into copulation sometime between 10:00 and 10:15 A. M. and remained in copula until sometime between 3:15 and 3:30 P. M., after falling to the ground at 2:15 P. M.

The sound level when both species of *Magicicada* were silent in the morning and evening fluctuated from about 47 to 50 decibels, and all readings in figures 6 and 7 above this were caused only by the sounds of *Magicicada*.   At the height of the *septendecim* chorus, about 9 to 11 A. M., and in the absence of *cassinii* chorusing, the sound level was about 55 to 60 decibels.   Occasional bursts of song by small groups of *cassinii* individuals caused temporary readings during the mornings as high as 65 to 70 decibels (not shown in fig. 6), but the maximum and minimum were read for *septendecim* as long as was possible both days.   After about 11:30 A. M. on June 18 and 9:45 A. M. on June 17 it was no longer possible to determine the intensity of the *septendecim* chorus because at these times the minimum readings on the sound level meter rose abruptly to a level above the maximum for *septendecim* due to the development of continuous chorusing by *cassinii*.   The bursts by *cassinii* in the morning occurred erratically and with little increase in
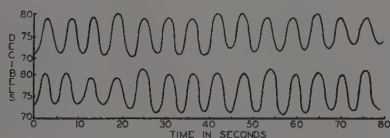
FIGURE 8   FIGURE 9

FIGURE 8.   The degree and regularity of fluctuation in sound intensity produced by a synchronized chorus of *M. cassinii*.
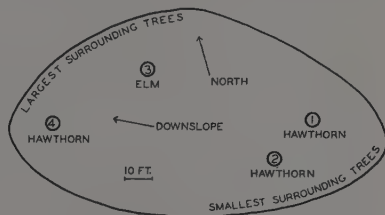
FIGURE 9.   Diagram of the clearing used in the song specificity tests, showing the location of the four cage trees and the general characteristics of the area.

rate or regularity but with gradually increasing intensity (more individuals involved).   On June 18 *cassinii* suddenly achieved synchrony at about 12:55 P. M. This synchrony was maintained until shortly after 5:00 P. M., when it gradually disappeared.   This is illustrated in figure 6 by both the height and the degree of separation of the maximum and minimum sound intensity readings.   When *septendecim* was in full chorus the fluctuation from maximum to minimum sound intensity was only 2 to 3 decibels at about 55 to 60 decibels. However, when *cassinii* was synchronized, the fluctuation was 8 to 12 decibels at about 70 to 80 decibels. These readings were taken 10 to 15 feet from the nearest singing individuals and in the area where *septendecim* was most abundant.   Table 1 shows the range and mean of sound intensity readings taken about six inches from ten singing and ten protesting individuals of both species.

The development of synchrony by *cassinii* was quite sudden on June 18 (fig. 6) and seemed puzzling at the time.   Plotting the data for June 18 revealed a distinct drop and rise in sunlight, temperature, and light intensity just prior to the development of synchrony by *cassinii*.   Whether or not this actually triggered the sudden development of synchrony is unknown.   However, the brief synchrony achieved on June 17 (fig. 7) occurred immediately following a similar fluctuation caused by a passing cloud.

Mutual stimulation.—The synchrony of *cassinii* and the development of chorusing through bursts of song by small groups of individuals demonstrates that *cassinii* is stimulated into song by hearing the singing of its own species. This was even more clearly demonstrated by playing continuous loops of tape recordings of various *cassinii* sounds to individuals released in Neotoma Valley, Hocking County, Ohio, where no seventeen-year cicadas occurred this year. The experiment was originally planned to test whether or not males and females could be attracted to a tape recorder. Unfortunately, shortly after the cicadas were released the weather became cloudy and little singing and practically no flying occurred for the rest of the day. The next two days were also rainy and cloudy, and on the third day and thereafter no cicadas could be heard or seen in the area. Due to other commitments the experiments could not be repeated. However, this cloudy weather, when the cicadas were singing little or not at all, provided an unexpected opportunity to test the possibility of stimulating cicadas into song with tape recordings.

Cicadas were released in approximately the following numbers: *septendecim*, 175 males, 100 females; *cassinii*, 250 males, 200 females. The cages containing the cicadas were upended on the edge of a woods bordered by tall weeds and sumac, and the sleeves were propped open, allowing the cicadas to crawl up and out onto the surrounding vegetation. The tape recorder and amplifier were set up on a small table about 30 feet away. The tapes played were recordings of Brood XIII made in Illinois in 1956 at 88 to 90° F, using a Magnemite Tape

TABLE 1

Maximum sound intensity in decibels about six inches from ten individuals of M. septendecim *and* M. cassinii

	cassinii		septendecim	
	congregational song	protest squawk	congregational song	protest squawk
range	87—99	85—94	70—78	70—79
mean	94.4	89.4	74.3	73.9

Recorder, Model 610–EV, with a tape speed of 15 inches per second, and an American Microphone Company Model D-33A Microphone. The tapes were played back with a PT63J Magnecorder, using a PT63–A2HZ Amplifier for the *septendecim* sounds, and a Jensen High Frequency Unit for the *cassinii* sounds. After some experimentation it was found that the released *cassinii* responded as well to the sounds played through the Magnecorder amplifier as to those played through the high frequency unit, though they were greatly distorted in frequency to the human ear.

The *septendecim* sounds played were as follows: (1) a single congregational song phrase repeated once every six seconds, (2) a single congregational song phrase repeated twice every five seconds, (3) a chorus dominated by a single individual, (4) a homogeneous chorus (no dominating individuals), (5) continuous protesting by a single individual, (6) courtship (short buzzes as in fig. 3) by a single individual. None of these sounds produced any apparent response from the *septendecim* individuals released in the area. They were played at 10 to 11 A. M. and again at 2 P. M. While the tapes were being played, *septendecim* males were singing intermittently and individually. The sound intensity from the recordings was 65 to 70 decibels near the released cicadas. The air temperature varied from 85 to 90° F in the area.

The *cassinii* sounds played were as follows: (1) a single complete congregational phrase repeated once every five seconds; (2) same, but with the intervals between ticks and buzzes removed, thus causing the phrase to be repeated twice every five seconds; (3) same as (1) but with the ticks in the phrase following the

buzz rather than preceding it; (4) continuous ticking by a single individual at a rate of 16 to 20 ticks per second (from the congregational song phrase); (5) a single congregational song phrase with the ticking removed, repeated once every four and one-half seconds; (6) same but with the interval removed, thus repeated at a rate of 2 to 3 buzzes every five seconds, (7) an unsynchronized chorus; (8) a synchronized chorus (12 phrases per minute); (9) continuous protesting by a single individual; (10) continuous courtship ticking by a single individual at a rate of four ticks per second; and (11) same but at a rate of six ticks per second. The sound intensity near the cicadas was 75 to 80 decibels. No individuals flew to the tape recorder. However, as the first *cassinii* sounds began to play, a strong increase in the singing of the released males was noticed, and subsequently every sound except the courtship ticking increased the chorusing of the released males. There was no response to tapes played at half speed, or to *septendecim* sounds, but response occurred to tapes played backward as well as to those played forward. The released males synchronized rather imperfectly with tapes (1), (5), and (8), and produced ticks in the interval between buzzes on tape (5). They sang asynchronously and continuously, though irregularly, with tapes (2), (3), (4), (6), (7), and (9). If the recorder was stopped suddenly in the middle of a buzz of any

TABLE 2

Numbers and kinds of cicadas in each of the tree cages on the test plot during each day of the test

Cage Day	1	2	3	4
June 1	31 silenced *septendecim* ♂	200 normal *septendecim* ♂	200 normal *cassinii* ♂	61 silenced *cassinii* ♂
June 4	100 normal *septendecim* ♀	200 normal *septendecim* ♂ 100 silenced *cassinii* ♂	200 normal *cassinii* ♂ 50 silenced *septendecim* ♂	200 normal *cassinii* ♀
June 5 June 6	200 normal *septendecim* ♀	200 normal *septendecim* ♂ 200 silenced *cassinii* ♂	200 normal *cassinii* ♂ 200 silenced *septendecim* ♂	200 normal *cassinii* ♀

kind, or immediately after a buzz, there was near silence for about a half second, and then the released males started ticking in chorus. If the recorder was not again turned on, only a few of the tickers finished with a buzz. When tape (1) was played backward, the released males began ticking immediately after the recorded ticks, then buzzed slightly behind the buzz on the tape. Thus, they were silent during the last part of the ticking on the tape, and ticked while the tape played silently.

These results indicate that hearing the cessation of the buzzing part of the congregational phrase stimulates ticking, and hearing the beginning of a buzz stimulates buzzing. At least a few individuals always followed a series of ticks with a buzz, even in the cloudy weather during the tests when the ticking was stimulated artificially. A part of the mechanism of synchronization is thus demonstrated by these results. It is possible that visual as well as auditory stimulation is involved in the synchrony of *cassinii*, part of the mechanism involving active synchronization of flight bursts and part of it involving active synchronization of sound bursts. This may be associated with the ease with which *cassinii* is disturbed into flight by nearby motion, and with its failure to synchronize except in high light intensity. It could also explain in part the failure of *cassinii* to accumulate on the outside of a cheesecloth-covered tree containing singing *cassinii*, since the cheesecloth would largely prevent mutual stimulation

and synchronization of flight bursts. The percentage of singers in a colony responding to a given rhythm probably depends on the intensity of the sound and climatic conditions. Further experimentation will be necessary to determine why *cassinii* does not achieve synchrony in the morning, though this may be dependent upon light intensity alone.

Tests on the Congregational Song as an Isolating Mechanism

Our observations to this point had suggested that the congregational song causes sexually responsive males and females to move into close proximity, and that the method of movement is chiefly through flight. This indicated that any test of this hypothesis would need to be conducted in an area in which the tested cicadas could fly freely and in which the light intensity was that normally encountered outside on a clear day. It was thus considered preferable to conduct the tests in the field, and the original plan was to secure large numbers of newly emerged adults, keep the sexes separate for a week or two, and then use these virgin adults in tests in an area in which no cicadas occurred this year. However, we were completely unsuccessful in keeping cicadas alive and vigorous in cages even though they were provided daily with freshly cut branches and leaves upon which to feed. Some feeding took place in the cages, but the adults died off rapidly; only a few living longer than a week and their vigor was much below normal. They sang very sporadically and only individually after being caged a few days. There was little flight in the cages which were approximately three feet on each side. This difficulty in keeping adult cicadas alive and vigorous in cages is not unusual. We found later, as did Beamer (1938) with various species of *Tibicen*, that it is possible to keep *Magicicada* adults in apparently normal condition in cheesecloth cages over branches of living trees. This indicates that the cicadas cannot feed satisfactorily on cut branches, perhaps because of a difference in turgor. Certainly feeding is an important consideration in spite of the surprising number of reports to the contrary in the literature. Cicadas can be observed feeding in great numbers in the field, and the defecation of a treeful of adults is like a continuous sprinkling rain. Cicadas which had remained vigorous in tree cages for a week died within two days after the trees upon which they were caged were sawed off near their bases, even though the trees were immediately placed in jars of water and did not wilt visibly until the second day. Two other tree cages of cicadas were set up at the same time and were left intact and the cicadas in these survived at least a week longer than those in the severed trees.

After these first failures it was impossible to secure virgin cicadas in numbers and with certainty from this brood. Consequently, an area was selected which contained both species in abundance and field tests were conducted to determine if uncaged cicadas from the natural population could be attracted to choruses by caged individuals, and if so, what evidence of specificity or lack of specificity of response could be obtained.

Description of test area. The test area for this portion of the study and for the sound intensity tests already described, is located eight miles southeast of Clarksburg, Ohio, on State Route 277 in South Union Township, Ross County. It is a hillside pasture, thickly overgrown with honey locust, walnut, and ash, 20 to 30 feet tall, and with hawthorn, crab apple, and elm, 4 to 20 feet tall. There is little or no underbrush and a ground cover of bluegrass occurs over most of the area. A few large old oaks are located within 100 to 200 yards of the test plot. This area was selected because it contained both species in great abundance and because there were no large trees in the immediate vicinity. This meant that (1) the cicadas could be collected in large numbers with little difficulty, and (2) cicadas caged in trees small enough to be covered with cheesecloth and observed would be more nearly on a level with the uncaged cicadas actively flying and singing outside.

Experimental procedure. An oval plot about 100 feet long and 50 feet wide

was cleared in the test area (fig. 9 and 10).   Four small trees about 10 to 12 feet tall and similar in size and shape were left and were covered with large cheese-cloth nets.   Into these cheesecloth cages were placed males and females of both species in the numbers and kinds indicated in table 2.   Control males were silenced by ripping their tymbals with a needle.   This did not appear to affect their behavior otherwise or to hasten their death.   While the normal males were singing, some of these silenced males were producing very weak sounds with their damaged tymbals and performing the other activities normally occurring during song.

After the cages had been filled with different kinds of cicadas on June 1, obser-vations were made on June 1, 4, and 5, to determine how many and what kinds of cicadas appeared on the outside of each of the cages during the day.   These results were correlated with climatic conditions, the activity of the uncaged cicadas, and the chorusing activity of the caged cicadas.   On June 6 the positions of cages 2 and 3 were reversed by sawing off the trees near their bases and tying them in place in the new locations, with the butts immersed in water.   Observations were made for one day (June 6) with these cages in the new locations to determine the effect of position of the cages both in the clearing and with respect to the cages containing females.   The results of the four days of observation are summarized in figures 11 to 16.

FIGURE 10.   Photograph of clearing facing downslope from southeast corner.

It was originally planned to use cages 1 and 4 as controls containing silenced males.   However, the silenced males were eventually placed in the test cages and those in cages 1 and 4 replaced with normal females.   Due to the smaller numbers of *septendecim* in the area, it was difficult to collect enough individuals to bring the numbers up to 200 in each of the cages.   However, as shown in figures 12 to 16, neither the fluctuations in numbers of cicadas in the different cages nor the reversing of position of cages 2 and 3 on June 6 had any large effect on the propor-tions of cicadas appearing on the outside of the cages.   The numbers of cicadas inside the cages were maintained by counting the dead cicadas in the bottoms of the cages each morning and replacing these with an equal number of freshly col-lected live cicadas.

On June 1 we attempted to estimate in what proportions the two species were present in the area immediately surrounding the clearing.   This was done by (1) circling the clearing on a cloudy morning, disturbing the bushes and trees as much as possible and then counting the numbers of cicadas which alighted on the

outsides of the cages, and (2) counting all the cicadas present on 50 different branches in the immediate surrounding area. In the first case we obtained a count of 93 *cassinii* and 11 *septendecim*. In the second case we counted 805 *cassinii* and *200 septendecim*. These estimates were subject to large errors. *Cassinii* is much more easily disturbed into flight than *septendecim* and this undoubtedly influenced the first count. Error in the second count was caused by the fact that *cassinii* individuals were usually congregated along the main trunks and in the tops of the trees while *septendecim* individuals were most abundant on the lower branches, the only place that we could make accurate counts. It is reasonable to expect that the actual proportions of *cassinii* individuals to *septendecim* individuals was somewhere between the proportions of 8:1 and 4:1 obtained in these instances.

During the early observations on June 1, all the cicadas were caused to fly from the outside of each cage after counting them each time. Later this procedure was abandoned because cicadas which moved only as far as the next cage distorted the readings on the other cages and because there was no way of knowing that the time lapse between our observations was sufficient to allow reorientation of the disturbed cicadas. Furthermore, it was noticed that only a few individuals alighted and just sat for any length of time on a cage. The only cicadas which remained around a particular cage for any length of time were individuals which were actively singing and flying and obviously being stimulated by the chorus coming from inside the cage. A few times small choruses were begun by *cassinii* males congregated on the outside of the *septendecim* cage, and vice versa. No attempt was made to break these up because they were always of a minor nature and it was reasoned that if the cage chorus was an attractant such small groups could not compete with the choruses inside the cages.

Before beginning the observations each day, the cicadas which had climbed or alighted upon the cages during the night were removed. The numbers of cicadas of both sexes and both species alighting on the outside of each of the cages were then determined at intervals by walking slowly around the cages and counting them from the ground. After collecting large numbers of these cicadas one becomes readily able to distinguish both the species and the sexes at some distance. Our accuracy was gauged by checking each other's counts several times, and each time the same numbers were obtained by both observers. The only source of error that appeared was in the possibility of counting some very small females of *septendecim* as females of *cassinii*, and accordingly a special effort was made to positively identify any doubtful females.

Results.—Figure 11 shows the climatic conditions during each of the four test days and the status of the natural and the cage choruses of both species. This figure will allow comparison of the results obtained in the cage tests with the more objective data in figures 6 and 7 concerning the effects of climatic conditions on chorusing activity. Unfortunately, the sound level meter was not available until several days after the cage tests had been completed and the importance of precise knowledge of fluctuations in climatic conditions was not apparent until the tests were nearly completed and the data plotted.

In assessing the significance of the various numbers and kinds of cicadas present at the cages at different times of day and on different days, the following factors should be considered: **1.** A slight increase should be expected in the numbers of cicadas of all kinds on all cages during the times that the uncaged cicadas were actively singing and flying. **2.** Cages 2 and 3, the test cages emitting choruses of *septendecim* and *cassinii*, respectively, had a few more cicadas perched on them than control cages 1 and 4, even when there was little or no chorusing inside or outside the cages. **3.** The actual numbers of cicadas attracted to the cages have little significance. The cages were competing with strong natural choruses. They were necessarily in unfavorable locations because they were in

small trees in a clearing and there is no information available as to the distance from which cicadas can be attracted by a chorus.   It is likely that the cage choruses influenced only those individuals flying near the cages, accidentally alighting on them, or singing in the nearest tree which in every case was 15 to 20 feet away. The cheesecloth not only lowered the light intensity inside the cages and thus reduced the intensity of the chorusing of the caged individuals, but also there are indications that it was less suitable as a perching place for singing individuals than tree leaves and branches.   Certainly the cheesecloth reduced contact between
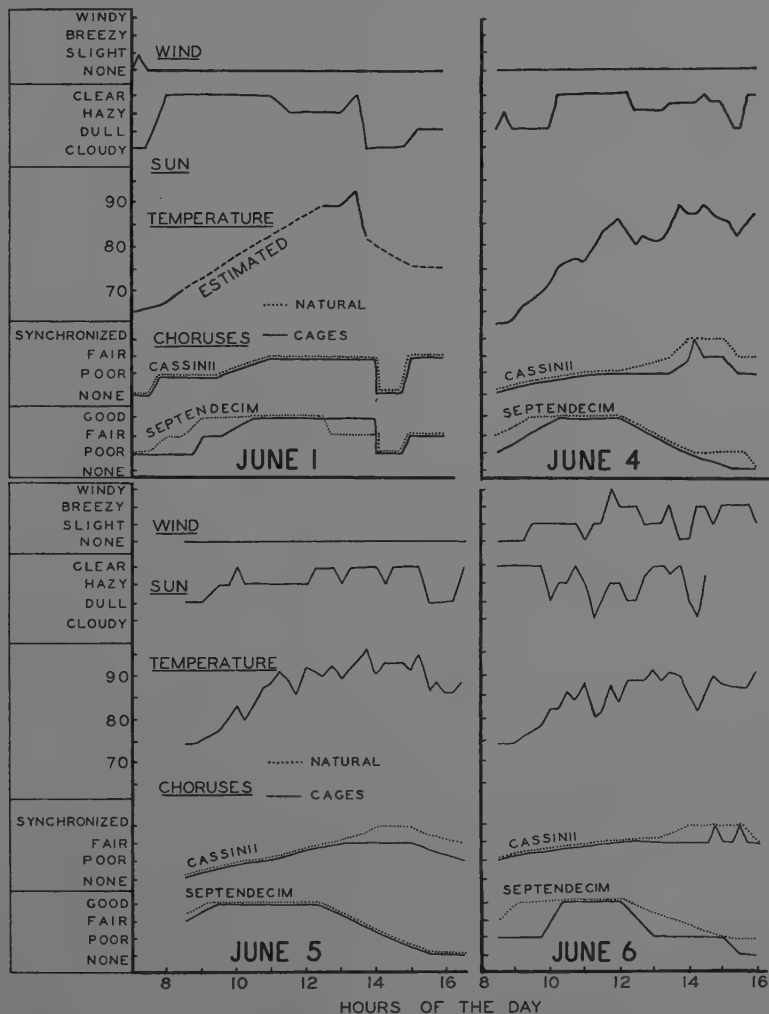
FIGURE 11.   Climatic conditions and status of the natural and cage choruses of *Magicicada* during the test days.

cicadas alighting on opposite sides of the tree and between the individuals inside and those outside the cage. For these reasons the data is given in terms of proportions of individuals of each species and each sex attracted to each cage (fig. 12 to 15) and proportions of the two species attracted to cages 2 and 3 (fig. 16). **4.** The activity of the cicadas on the outside of a cage, though not transmitted in figures 12 to 16, was frequently more important than the numbers of cicadas involved. Nearly all *septendecim* males remaining on the outside of cage 2, and
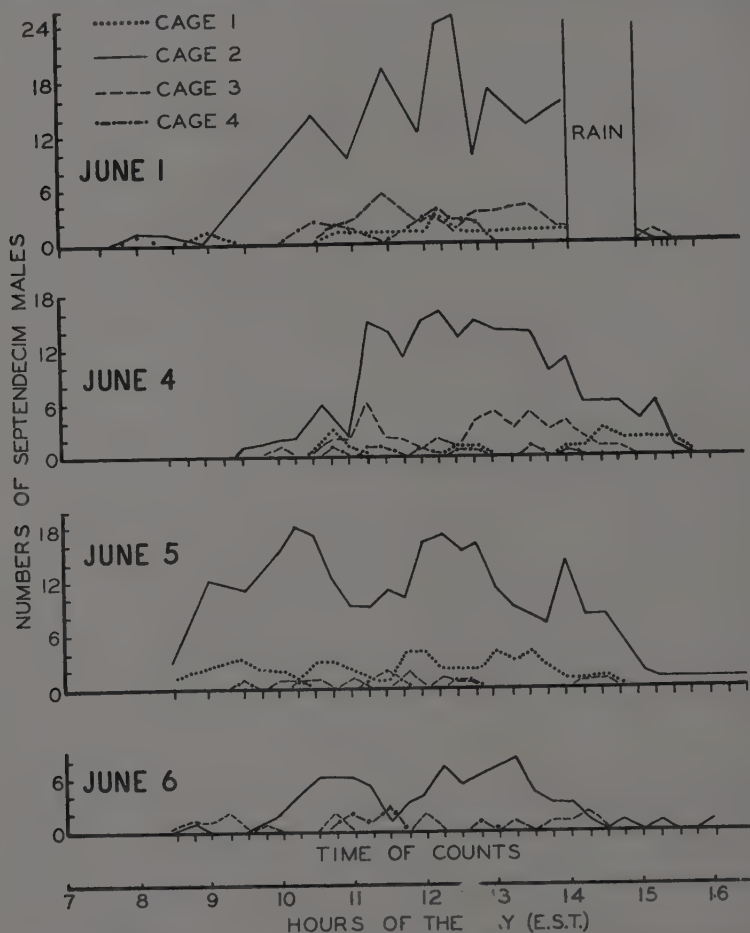
FIGURE 12. Numbers of males of *septendecim* at each cage at intervals throughout each of the test days.

cassinii males remaining on the outside of cage 3, were pursuing and courting females or singing and flying. The *cassinii* males on the outside of cage 2 and *septendecim* males on the outside of cage 3 either were not performing these activities or their stay on the cage was brief. Five instances of *septendecim* copulation were

noted on cage 2 and one on cage 1; one instance of *cassinii* copulation was noted on cage 3. No other cases were observed. Many *septendecim* individuals were missed in the counts on cage 2 because they had fallen to the ground scuffling. **5**. The tests were initiated 7 to 10 days after strong chorusing by both species had begun. The large numbers of ovipositing females observed suggests that the proportion of virgin females in the area was low. This probably accounts for poor test results with females and may have caused a slight increase in the numbers of responding males.

As indicated in figures 12 to 15, the most positive data were obtained with males of *septendecim* (fig. 12). These cicadas were attracted to cage 2 in considerably higher numbers than to any other cage, even higher than to cage 1 only fifteen
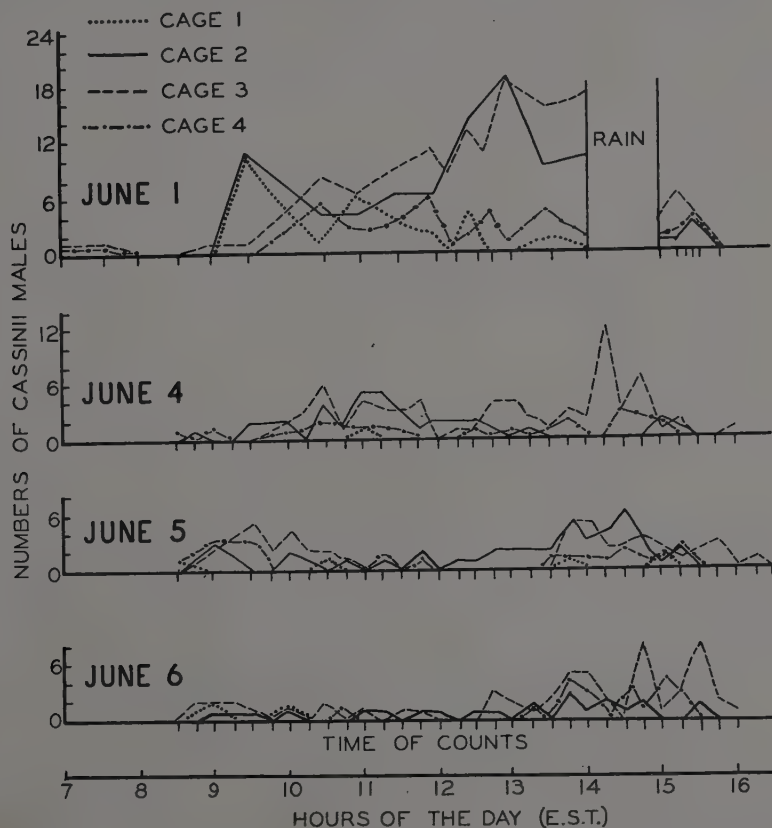
FIGURE 13. Numbers of males of *cassinii* at each cage at intervals throughout each of the test days.

feet away and containing 200 *septendecim* females. The largest numbers of individuals began to accumulate on cage 2 at about the time the cage was estimated to be developing a strong chorus (fig. 11). The subjectivity of the evaluation of the status of the cage choruses prevents precise comparison of the time

of these two events.   A slight increase in numbers of cicadas on the outside of the cages occurred just prior to the development of strong choruses inside the cages due to the fact that the natural choruses generally developed before the cage choruses and caused an increase in the flying activity of the uncaged cicadas.

Cage 1 shows a slightly higher number of *septendecim* males than cages 3 and 4, apparently because of a kind of "overflow" of singing, flying males obviously being stimulated by the chorus in cage 2. On June 6, when the cage containing the *septendecim* chorus was moved away from the cage containing *septendecim* females, the latter showed not a single male at any time during the day though there should have been more sexually responsive females inside the cage than at any previous time. On June 5 the consistently higher number of *septendecim* males on cage 1 was due to a cluster of two to four males which remained on the cheesecloth directly opposite a group of three *septendecim* females for nearly the whole day. These were apparently sexually responsive females and this seems to demonstrate that a sexually responsive female in very close proximity to a male is more attractive than a nearby strong chorus by males.
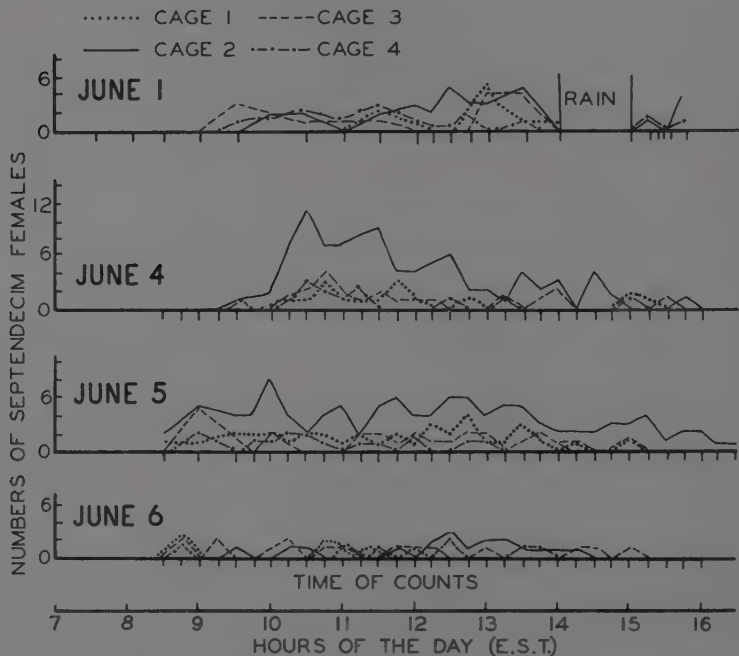
FIGURE 14.   Numbers of females of *septendecim* at each cage at intervals throughout each of the test days.

As illustrated in figure 13, cage 3 was much less successful in attracting *cassinii* males than cage 2 was in attracting *septendecim* males. Although the proportions of *cassinii* individuals at this cage were usually much higher than should have been expected on the basis of estimated proportions of individuals in the total population (fig. 16), at only three times was the number of males of

cassinii much higher at cage 3 than at any other cage. These times were at 2:15 P. M. on June 4 and at 2:30 and 3:30 P. M. on June 6. Upon examining figure 11, we noted that these were the only times that the caged *cassinii* were in synchrony with the natural chorus. At no time did the caged *cassinii* achieve synchrony within the cage and not with the natural chorus. This seems to demonstrate that the pulsations in total sound intensity produced by a synchronized chorus of *cassinii* are correlated with the effectiveness of the sound as an attractant to *cassinii* individuals.
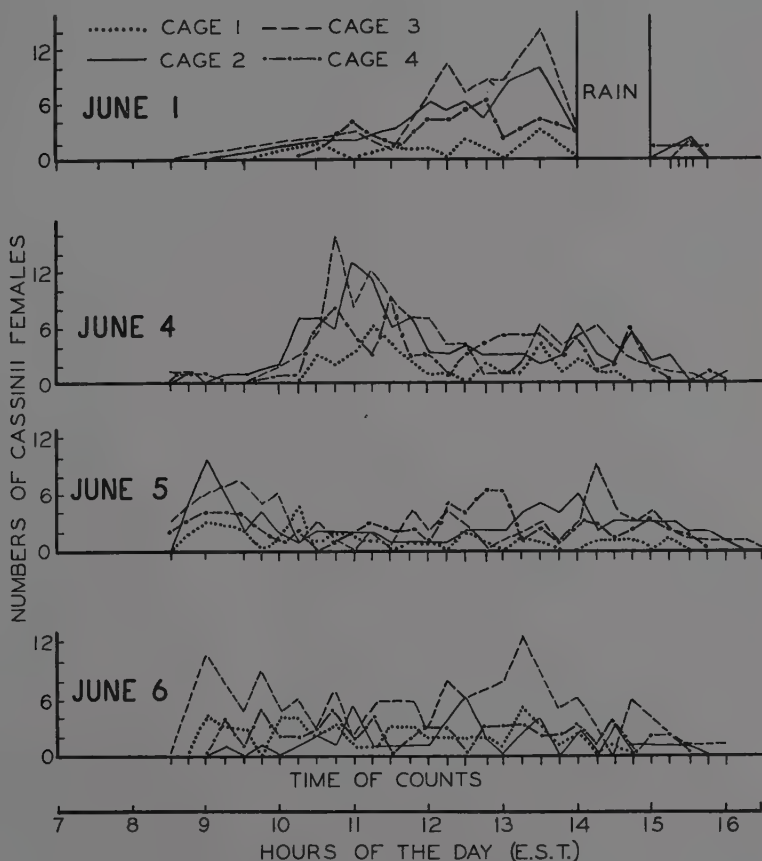
FIGURE 15. Numbers of females of *cassinii* at each cage at intervals throughout each of the test days.

There are several factors which may be involved in the general failure of the caged *cassinii* to develop synchrony and to attract more individuals. The natural *cassinii* chorus was much stronger in relation to the cage chorus than the natural *septendecim* chorus to its cage chorus. Cage 3 was in a less favorable location than cage 2, as is shown by the results obtained for both cages on June 6 when their positions were reversed. This was partly due to the original cage 3 location

being farther from the edge of the clearing and partly due to its being shorter in relation to the surrounding trees (fig. 9). In addition, singing and flying *cassinii* individuals congregate near the tops of trees while *septendecim* is usually found on the lower branches. *Cassinii* individuals flying over the clearing were usually 20 feet above the top of cage 2. Finally, the lowered light intensity inside the cheesecloth had a greater effect on the chorusing of the caged *cassinii* than on the chorusing of the caged *septendecim*.

In addition to the immediate effects of cloudy, rainy weather on the activity of *Magicicada* (fig. 11), another, cumulative effect may be visible in the results shown in figure 14. Just prior to June 1 there had been several days of fair weather during which it can be assumed that both species were chorusing well and sexually responsive females were having little difficulty in encountering
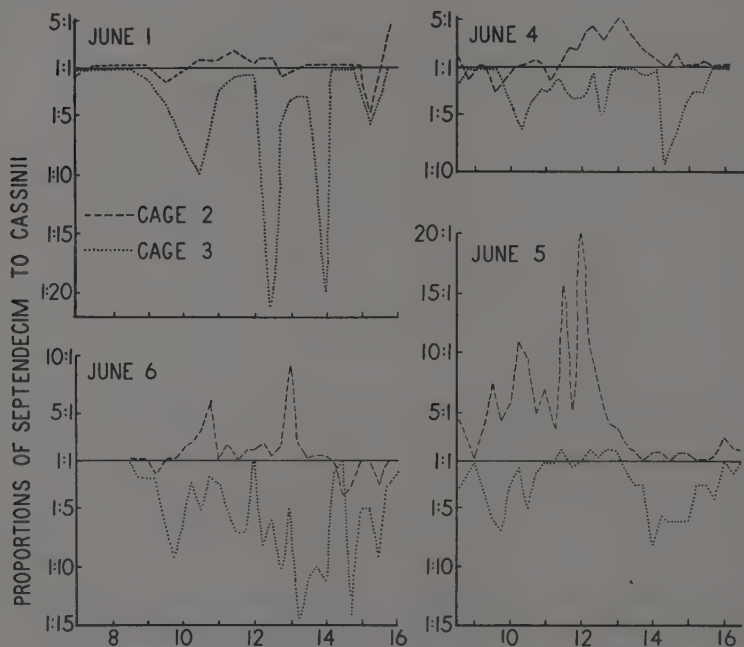
FIGURE 16. Proportions of individuals of *M. septendecim* and *M. cassinii* at cages 2 and 3 at intervals throughout each of the test days (all zeros are considered as ones).

sexually responsive males. None of the results with females were as good as those with males and it is possible that this was due to a low incidence of virgin females during the tests, as already suggested. A few cloudy, rainy days, however, should have the effect of increasing the proportion of sexually responsive females in an area because of the presence of newly emerged females and perhaps because of previously mated females again becoming sexually responsive. During June 2 and 3, as well as during part of June 1, it was cloudy and rainy and there was little chorusing activity. As shown in figure 14, a considerable number of *septendecim* females was attracted to cage 2 on June 4 and this number then dropped gradually the next two days. Likewise, the number of *septendecim*

males attracted to cage 2 (fig. 12) was greater on June 1 and 5 than on June 4, which is what would be expected if more sexually responsive females occurred in the area on June 4.   The results obtained on June 6 are difficult to compare with those obtained on the other three days because of the reversal of the locations of cages 2 and 3.

The failure of the results obtained with *cassinii* females (fig. 15) to compare with those obtained for *septendecim* females (fig. 14) is probably due to a combination of the general failure to attract large numbers of *cassinii* individuals and the low number of attracted females of both species.   It is probable that the June 1 data for *cassinii* males and females both are positive, this being obscured by the more favorable location of cage 2 for both cicadas.

A peak of activity by the females of each species also occurred on most days sometime prior to the peak of chorusing activity of the males.   The only apparent explanation for this is that it was caused by females moving about prior to oviposition.

Figure 16 shows the proportions of individuals of the two species at the test cages, 2 and 3.   A comparison of these proportions with the proportions expected through chance alone on the basis of the counts on June 1 (4 to 8 *cassinii* to 1 *septendecim*) gives a clear indication of the consistently positive results of the test. The lines for the two cages cross only once and approach each other rarely except early and late in the day when the cicadas were not active and the numbers on the cages approached zero.   All large deviations were toward higher proportions of *septendecim* at cage 2 and higher proportions of *cassinii* at cage 3.

DISCUSSION

Although there have been numerous speculations as to the probable functions or lack of functions of the songs of cicadas, there have been practically no experimental investigations on the problem and none of those previously conducted have yielded positive results.   In the voluminous literature dealing with the periodical cicadas only three examples are known to the writers in which some significant observation concerning this problem or some evidence based on experimentation has been presented.   In 1937 Cory and Knight stated, "The cicada's song, transmitted over a carbon microphone to a loud speaker in an adjoining room, failed to orient significant numbers of virgin females."   This brief report cannot be evaluated, however, because it is not known which song of which species was used, which species of virgin females was used, how old these virgins were, at what temperature the song was recorded, the temperature of the room containing the virgin females, what the light intensity of the room was, at what intensity the sound was played to the females, or whether or not the females could fly in the enclosure in which they were housed.   Likewise, it is not known how long the females had been caged, or whether or not, or how, they had been fed.

In 1941 Craig speculated that periodical cicadas fly toward the greatest volume of sound and that this could account for their frequently surprisingly definite limits of distribution.   This suggestion is in agreement with the results of the present study.

In 1946 Allard noted the synchronization of *cassinii* and described it accurately. This observation alone established the existence of behaviorally significant differences between the songs of the two species.   Field observations of this sort have too frequently been ignored in the present surge of experimental studies on the auditory capacities of insects, some of which have led to the suggestion that insects respond indiscriminately to nearly any sound as long as it contains certain structural elements which are common to almost all animal sounds.   As mentioned in an earlier paper (Alexander, 1956), this conclusion has seemed generally unwarranted due to a number of phenomena repeatedly observable in the laboratory and field behavior of singing Orthoptera and Cicadidae.   A series of well-designed

experiments by Walker (1958) with different species of tree crickets in the eastern United States reveals highly discriminatory capacities in these insects and shows that the females of a given species respond only to the song of the males of their own species and not to those of any other species occurring in the same locality. There is every indication that such sensitivity is the rule in groups of insects which live together and in which song is the principal force bringing the adult males and females into breeding proximity.[1]   Song has proven to be the most valuable species recognition character available in the singing Orthoptera and Cicadidae, and it is here suggested that taxonomists puzzling over morphologically ill-defined species in other sexually reproducing animals might do well to search for the mechanism responsible for bringing the sexes together in their particular groups.   In some cases this character may be behavioral, in others it may be ecological, and in others it may be a complex combination (Alexander, 1957a).   It might be something as obscure and remote as the odor of a host plant to a female ready to oviposit.   In any case, it seems logical to expect a high degree of selective value to be attached to uniqueness in characteristics which are responsible for this kind of intraspecific congregation and, concomitantly, interspecific isolation.   Such mechanisms can perhaps be regarded as the least wasteful of all possible isolating mechanisms, preventing interspecific encounters as well as wasted time and energy as a result of such encounters.

The sensitivity demonstrated in tree crickets by Walker and in two species of *Magicicada* in the present study indicates that the failure of past investigators to obtain positive results in similar experiments may have been due to failure to expect a sufficient degree of sensitivity, and thus failure to design an experiment in which such important variables as temperature, sound intensity, light intensity, and physiological condition of the test animals were properly taken into account. It seems evident that experiments with sounds which do not remotely resemble in rhythm those sounds to which the animal is subjected in nature have little or no bearing on the sensitivity of the particular animal to slight fluctuations in the rhythm of natural sounds.   In such experiments, an entirely different kind of sensitivity is apparently being tested.   The sensitivity demonstrated in the species tested so far with respect to natural sounds indicates that investigators working with the idea of eventually controlling an insect or altering its behavior toward some practical end will most profitably concern themselves initially with rhythm structures which fall within the narrow range which the animal encounters and to which it responds in nature.

SUMMARY

Observational and experimental field studies carried out in southern Ohio on Brood XIV of the seventeen-year cicadas, *Magicicada septendecim* (Linnaeus) and *M. cassinii* (Fisher), together with data gathered during the emergence of the same two species in Brood XIII in northern Illinois, have led to the following conclusions:

1.   The whole mode of life of the seventeen-year cicadas (as also seems likely with other singing insects) is so completely tied up with the system of sound communication of the adults that an understanding of their behavior, ecology, distribution, history, and taxonomic relationships is impossible without a knowledge of how this system operates.

2.   The males of each species have at least four distinct sound responses: (1)

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[1]Since submission of this manuscript, the following publication has appeared: Perdeck, A. C. 1957.   The isolating value of specific song patterns in two sibling species of grasshoppers (*Chorthippus brunneus* Thunb. and *C. biguttulus* L.) [Orthoptera: Acrididae: Acridinae.] Leiden, Netherlands: E. J. Brill, publ., 75 pp., 9 fig., 28 tab.   Perdeck's, Walker's, and the present report together confirm that species-specific song patterns operate as isolating mechanisms among closely related sympatric species in all three of the major systems of sound communication occurring in insects.

a congregational song, the production of which is regulated by daily fluctuations in climatic conditions and by hearing the songs produced by other males, (2) and (3) two courtship sounds, produced at different stages of courtship, and though apparently not produced prior to every instance of copulation probably always terminating in copulation when the female is responsive, and (4) a protest squawk, so named because it is produced by individuals captured, held, disturbed into flight, or otherwise irritated.

3.   In each species these sounds are radically different in rhythm and frequency from the sounds produced by the other species in the same situations, yet the structural inter-relationships of the sounds of one species are in general analogous to the structural inter-relationships of the sounds of the other species.

4.   The congregational song is the only sound produced in chorus, and in both species chorusing is most successful on clear, windless days, and least successful on cloudy, rainy days.

5.   The chorusing behavior of the two species is different: *cassinii* individuals synchronize their songs while *septendecim* individuals do not, and their peaks of chorusing activity occur at different times during the day.

6.   The differences in the chorusing behavior of the two species, as well as the structural differences in the songs of individuals, are behaviorally significant to both males and females.

7.   The congregational song is properly named because it acts as a congregating mechanism for both males and females of each species and concomitantly reduces the number of interspecific encounters between sexually responsive males and females.   It is probable that a visual stimulus is also involved in the achievement of chorus synchrony by *cassinii* and thus in congregation since the congregational chorus seems effective only when synchrony is achieved.

8.   The chief method of congregation is through flight, and the short bursts of flight incorporated into the rhythm of the congregational chorusing facilitate this congregation, increasing the possibility that a sexually responsive female will encounter a male and decreasing the length of time involved.

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DIROFILARIA SCAPICEPS FROM THE RABBIT (*SYLVILAGUS FLORIDANUS MEARNSI*) IN OHIO

(NEMATODA: DIPETALONEMATIDAE)

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Several surveys of parasites from rabbits have been made in the United States in past years, but records of filariae are scarce. *Dirofilaria scapiceps* has not been reported from Ohio.

Leidy (1866) found filarial worms under the skin of the hind foot of *Lepus sylvaticus* (*Sylvilagus floridanus mallurus*). He named these worms *Filaria scapiceps*. The locality of Leidy's collection is not given, but Hall (1916) believed that Leidy probably collected them in Pennsylvania. Hall reported two other cases, one from *Lepus campestris*, locality not given, and another collected by Douthitt from *Sylvilagus floridanus alacer* at Sulphur Springs, Oklahoma. The parasites collected by Douthitt were found under the skin of the lumbar region. In 1927, Harkin reported microfilariae in the blood of a rabbit from British Columbia.

Alicata (1929) recorded a previously unreported case from a rabbit collected in 1916. In this case, the adult nematodes were inside the tarsus of *Sylvilagus floridanus mallurus* from Woodford, Virginia. He also reported worms from inside the tarsus of the hind leg of what was probably the marsh rabbit, *Sylvilagus palustris*, from Kingston, North Carolina. Schwartz and Alicata (1931) described microfilariae from the blood of *Lepus washingtonii* collected in Washington State. MacLulich (1937) found *Dirofilaria scapiceps* adults in *Lepus americanus* in Ontario.

Manweiler (1938) found this parasitic nematode in the snowshoe hare, *Lepus americanus phaeonotus* in Minnesota. About one-third of all the snowshoe hares collected by Manweiler during the winters of 1936–1937 and 1937–1938 were infected. He found the incidence increased from October to February and then decreased to July. Highby (1938) observed microfilariae in the blood of a snowshoe hare in Minnesota. Wild mosquitoes were allowed to feed on this rabbit. Twelve days after this feeding, infective stages were seen actively moving within the proboscides of the mosquitoes. Microfilariae were also observed in the gut contents of an engorged tick. In 1943, Highby reported 23 cases of infection from 57 snowshoe hares examined in Minnesota. He found that the incidence varied from 13 to 58 percent in animals collected from three geographic extremes of the hosts' range. Highby also demonstrated that five species of mosquitoes (*Aedes canadensis, A. cinereus, A. excursians, A. fitchii*, and *A. verlans*) were susceptible as hosts to complete larval development. Transmission through the mosquito from the snowshoe hare to a domestic rabbit was accomplished.

Llewellyn and Handley (1945) found a small percentage of rabbits infected with this parasite in Virginia. They sent infected rabbits to Bell and Chalgren of U.S.P.H.S. for parasite identification. The nematodes were found in the intermuscular fasciae of the hind legs except for one from the subcutaneous fasciae of the back just posterior to the shoulder. Penner, Dery, and Knuckles (1953) examined four cottontails which were apparently *Sylvilagus floridanus mallurus* from Connecticut. Three of the four rabbits examined contained microfilariae in the blood, but these workers were able to recover only a single pair of adults from the left rear foot near the Achille's tendon of one of the rabbits. These same workers identified, as *D. scapiceps*, five adult nematodes from the hind leg of a cottontail rabbit killed in Massachusetts.

Erickson (1947) examined 97 cottontails for parasites, and reported 15 different helminth species, but even though the leg joints of 30 rabbits were carefully examined, *Dirofilaria scapiceps* was not found.   In studies made by Clancy, Jungherr, and Sime (1940) filariae were not reported from 342 cottontail rabbits examined for parasites.   Cheatum, working in New York State, examined 937 cottontails but found no *D. scapiceps*.   Several studies of population fluctuation have been made for rabbits in Ohio.   Some of these involved an examination of animal parasites, but there was no record of filarial worms.   Phinney (1956) x-rayed the legs of 78 rabbits from Ohio, in a study of aging techniques, but he never observed nematodes in the legs.

We obtained our specimens from two *Sylvilagus floridanus mearnsi* which were shot by Mr. Phinney and Mr. Loren Mosely in the Zaleski State Forest, Madison Township, Vinton County, Ohio, in December, 1955.   Each of these two rabbits had a large swelling on the left hind foot.   When these swellings were incised, they were found to be filled with large filarial worms (fig. 1).   The nematodes were in the intermuscular fasciae of the hock of the foot, and in the joint between the tibia, fibula and tarsal bones.   Seventy-six nematodes were removed from one rabbit and there were 84 in the tissues of the other.   We have identified these parasites as *Dirofilaria scapiceps* (Leidy, 1886) Railliet and Henry, 1911.

FIGURE 1.   Nematodes protruding from the intermuscular fasciae of the hock of the left rear leg.

The males range from 11 to 16 mm in length and from 305 to 375 microns in width.   The left spicule is 113 to 139 microns long and the right spicule is 84 to 86 microns in length.   The females are 25 to 30 mm long and 745 to 765 microns wide.   The vulva is located approximately 1.5 mm from the anterior end.   The embryos are slender and filiform.

There has been some importation of cottontail rabbits from other states into Ohio in the past; however, the importation has been from states where this nematode has not been reported.   It seems probable that these nematodes have been parasitizing rabbits in Ohio for many years.   The pathology is not well known; Schwartz and Alicata (1931) reported one rabbit with microfilariae which appeared to be in a stupor.   The adult nematodes did not seem to disturb the movement of cottontails collected in Ohio, but the effect of adults over a long period of time should be studied.   Careful examination of fresh blood smears and leg joints should reveal the incidence and distribution of this parasite in Ohio.

With this report *Dirofilaria scapiceps* has been recorded from wild rabbits of ten states in the United States and from two provinces of Canada.   In the United States it is known in Pennsylvania, Oklahoma, Virginia, North Carolina,

Minnesota, Washington, Wisconsin, Connecticut, Massachusetts, and Ohio, and in Canada from British Columbia and Ontario.

Specimens collected in Ohio are deposited in the Helminthological Collection, Department of Zoology and Entomology, The Ohio State University.

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